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Nonhuman Primates as Models of Hemispheric Specialization

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As a result of his observation that the understanding of human cognition derives mostly from the study of human adults, Terrace (1993) called for the development of comparative psychology in the field of cognitive sciences. According to Terrace, "the study of cognitive processes in animals provides a unique opportunity to investigate the phylogeny and ontogeny of cognition" (Terrace, 1993, p. 162). There are several aspects of human cognition (e.g., list learning and imagery) that can be investigated by the use of nonverbal tasks. Psychologists' work with pigeons and monkeys (e.g., for chunking in memory, Terrace, 1987; for serial learning, Terrace, 1991; for imagery, Hollard & Delius, 1982; Neiworth & Rilling, 1987; Vauclair, Fagot, & Hopkins, 1993) has suggested that these complex cognitive skills are both independent from language and phylogenetically old. It is thus interesting to study animal cognition to understand the processes of human cognition that do not presuppose language and, more generally, to address the nature of nonverbal thought (Roitblat, 1987; Vauclair, 1996). In this context, nonhuman primates are worth studying because these species are closest to humans in their anatomy and physiology, as well as in their motor and perceptual processing. Nonhuman primates are also good candidates to test the phylogenetic validity of human-based models of cognition (see also Fujita, 1997).

The present chapter concerns the issue of hemispheric specialization for perceptual and cognitive processes. In spite of a long-lasting view that only humans are lateralized (e.g., Warren, 1980), there is now strong documentation for anatomical lateralizations, functional lateralizations, or both in several animal taxa, including birds, rodents, and nonhuman primates (see Bradshaw & Rogers, 1993; Hellige, 1993). We selectively report demonstrations from studies of nonhuman primates. After a short review of the evidence for structural (anatomical) lateralization, we describe the

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methods used by neuropsychologists and psychologists to investigate functional lateralization in primates, and then we present some evidence for cerebral lateralization in monkeys and apes. Finally, we delineate the interests and limits of a primate model of cerebral asymmetry.

In the interest of space, we do not discuss motor asymmetries in detail here (see, for a review, Ward & Hopkins, 1993). Note, however, that although this topic remains controversial, several authors (e.g., Fagot & Vauclair, 1991; MacNeilage, Studdert-Kennedy, & Lindblom, 1987) reported the existence of population biases for hand preference in nonhuman primate species. Hopkins (1995, 1996) found a significant right-hand preference in a large sample of captive chimpanzees for bipedal reaching, bimanual feeding, throwing, and a coordinated bimanual task. These data suggest a phylogenetic continuity for handedness in primate species, at least between apes and humans.

Evidence for Neuroanatomical Asymmetries in Nonhuman Primates

Several left-right anatomical differences have been reported in apes and monkeys. For example, the left Sylvian fissure is longer than the right in chimpanzees (Pan troglodytes: Yeni-Komshian & Benson, 1976) and in macaques (Macaca mulatta: Falk, Cheverud, Vannier, & Conroy, 1986). Other asymmetries have been observed in the temporal planum and in the frontal lobe. Thus, the left planum of chimpanzees is, like that of humans, larger than the right (Gannon, Holloway, Broadfield, & Braun, 1998; Witelson, 1977). By contrast, there is in baboons (Papio papio: Cain & Wada, 1979), chimpanzees, gorillas (Gorilla gorilla), and humans (LeMay, 1976; Zilles et al., 1996) a protrusion of the right frontal lobe. In general terms, these studies suggest that anatomical asymmetries of nonhuman primates tend to be similar to those of right-handed humans, even though asymmetries are stronger in humans and apes than in monkeys. If the exact relation between structural and functional asymmetries remains unknown, it is likely that a connection exists between these two levels of asymmetry. Hence, it is probably more than a coincidence that the planum temporal is larger on the left side than on the right side of the human brain, as this structure on the left side includes the Wernicke area, which is involved in language comprehension.

Evidence for Functional Asymmetries in Nonhuman Primates

In this section we present empirical evidence for behavioral lateralization in nonhuman primates in visual and auditory tasks. In Japanese macaques (Macaca fuscata), a right-ear (left-hemisphere) advantage was found to discriminate vocalizations of conspecifics (Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978). Implication of the left hemisphere for this kind of auditory discrimination was confirmed by lesion studies (Heffner

& Heffner, 1984). Because species different from Japanese macaques did not exhibit such asymmetries when they were tested with the Japanese macaques calls (Petersen et al., 1978), results suggest that signals have to convey signification to elicit cerebral lateralization.

Visuospatial tasks also revealed cognitive lateralization in primates. Thus, the left hemisphere of split-brain macaques was better than the right for discriminating line orientations (Hamilton & Vermeire, 1988). Jason, Cowey, and Weiskrantz (1984) observed that monkeys exhibited a left-hemisphere advantage when they had to report whether a dot was depicted in the center of a square. Evidence for a right-hemisphere advantage in visuospatial tasks comes from studies with split-brain macaques (Macaca mulatta) involving face discrimination (Hamilton & Vermeire, 1988). Morris and Hopkins (1993) used chimeric stimuli to demonstrate in two intact chimpanzees a right-hemisphere advantage for recognizing human and facial expressions ("happy" vs. "neutral" face). In addition, Ifune, Vermeire, and Hamilton (1984) found that split-brain macaques displayed more facial expressions toward video clips picturing humans and monkeys when the movies were presented to the right hemisphere. Finally, Hauser (1993) showed that facial expressions of fear and threat in rhesus monkeys were stronger on the left side of the face (primarily under the control of the right hemisphere) compared with the right (left hemisphere). In sum, the right hemisphere of monkeys appears to be specialized for perceiving emotional behaviors as well as for producing them. Similar right-hemispheric specializations for emotions were reported in humans (see Bradshaw & Rogers, 1993).

Which conclusion can be drawn from the literature on hemispheric lateralization? It appears that the existence of hemispheric asymmetries per se is neither specific to humans nor dependent on language. Consistent with this position, functional asymmetries (e.g., for face recognition) were found in human babies well before language acquisition (see references in Young & Ellis, 1989). Also, it is worth noticing that human and nonhuman primates show a remarkable convergence in their morphological and structural laterality. Thus, anatomical asymmetries of the Sylvian fissure are identical in apes and humans, although less pronounced in the former species.

At the functional level, face discrimination seems to be lateralized in the same way in several primate species. A consistent right-hemisphere advantage was found in monkeys, apes, and humans. Moreover, there is an advantage for the left hemisphere in Japanese macaques for processing communicatively significant auditory signals. Such a specialization evokes lateralization for speech processing in humans. Notwithstanding these similarities, there are some known differences between humans and other primates. For instance, Hamilton and Vermeire (1988) reported a left-hemisphere advantage for line orientation discrimination in split-brain macaques, a task that generally favors the right hemisphere in humans (Hellige, 1993). The demonstration of structural and functional asymmetries in primates (but also in other vertebrates; see Bradshaw & Rogers, 1993) corresponds to the idea that human laterality has phylogenetic roots. In fact, lateralization appears to represent a fundamental feature of the neuroanatomy and behavior in both animals and humans (Geschwind & Galaburda, 1985).

A Nonhuman Primate Model of Cerebral Asymmetry: Experimental Paradigms

In the study of cognitive hemispheric asymmetries in nonhuman primates, the traditional approach consists of either lesioning the brain unilaterally or splitting the two cerebral hemispheres by cutting the corpus callosum and accompanying posterior and anterior commissures. Such studies offer valuable data that complement the literature on brain-lesioned human participants. Nevertheless, they tell little about the intact brain and thus are of limited heuristic value for understanding its functioning. Consequently, there is a need for developing behavioral methods that would be adapted for the comparative investigation of intact human and nonhuman primates.

In the field of human vision, researchers interested in hemispheric lateralization have repeatedly used a tachistoscope (Hellige, 1993). The use of the tachistoscope implies, first, centration of the gaze on a fixation point and, second, the short display of a stimulus in either the left or the right visual half-field. Given the anatomy of the visual system, visual information presented with a sufficient eccentricity (more than 2.5°) relative to the fixation point is directed to the hemisphere that is opposite to the stimulated half-field (Bryden, 1982). It is thus possible with that method to selectively activate the left or the right hemisphere of the intact brain.

Following Washburn, Hopkins, and Rumbaugh (1989), we developed for humans and baboons a test procedure that has several characteristics in common with the use of a tachistoscope (Vauclair, Fagot, & Hopkins, 1993). During this procedure, primates are initially trained to manipulate a joystick, so as to displace a cursor in any direction on a computer monitor (see Figure 16.1). They are then tested in a matching-to-sample task in which the sample form is presented to either the left or the right of a fixation point for a duration shorter (e.g., 120 ms) than the latency to initiate a visual saccade (Wilde, Vauclair, & Fagot, 1994). To ensure that the sample form is presented in one visual half-field only, the researcher imposes fixation by having the subject place and maintain the cursor on the fixation point before the display of the sample form. Therefore, this technique is analogous to the tachistoscopic mode of stimulus presentation. It restricts the visual input to one visual half-field to transfer the information to the contralateral hemisphere.

This system is advantageous because it can be adapted for testing both human and nonhuman participants in strictly identical experimental conditions. Because there is no need for linguistic instructions, it is also ideal for participants, such as those with aphasia, whose language functions are deficient. In our experiments, humans and baboons are tested with the same stimuli and procedure. Use of identical procedures does not equate

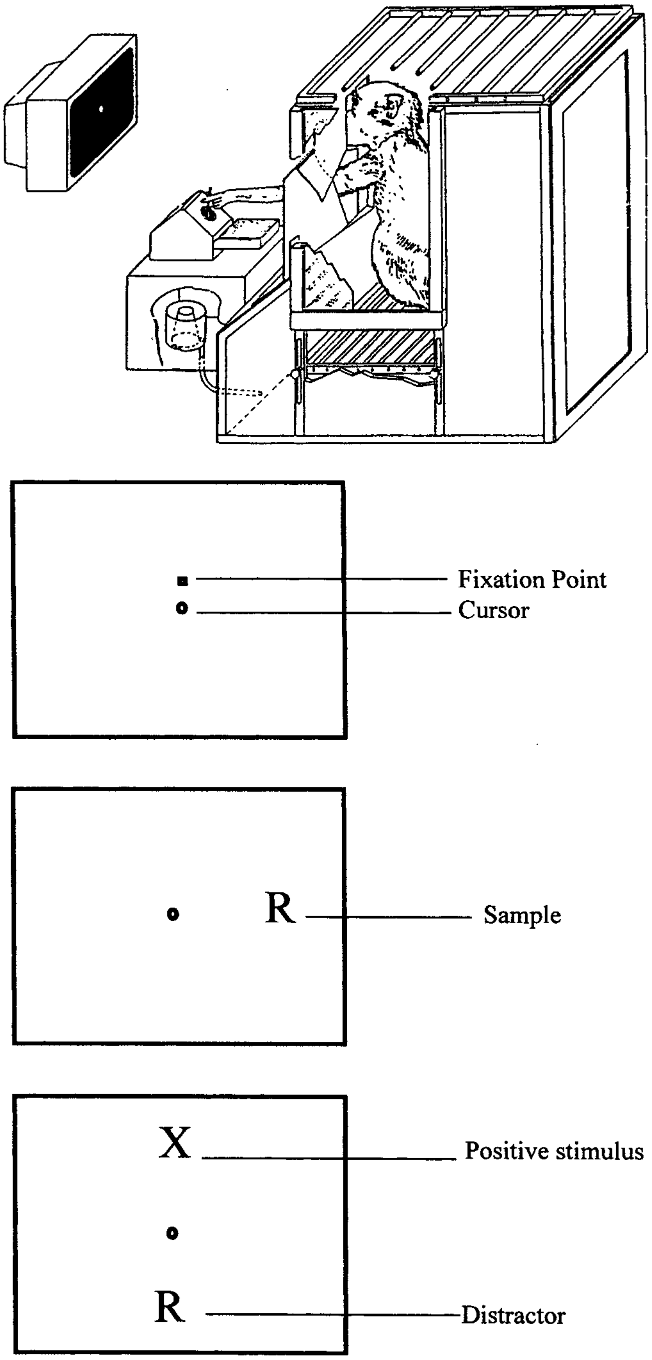

Figure 16.1. Illustration of the divided-field procedure and stimuli used during the comparative assessment of visual asymmetry in primates. Top: the apparatus used with monkeys. Bottom: the three phases of each testing trial: (a) presentation of the cursor and fixation point on the screen, (b) lateral presentation of the sample stimulus, and (c) presentation of the recognition display.

all the factors that may affect the results-for instance, the attentional, memory, and motivational factors. Nevertheless, testing humans and monkeys with similar procedures is a reasonable approach to tapping species' differences and similarities in hemispheric processing. Two sets of studies illustrate our approach and its heuristic value.

The first set of experiments was aimed at comparing the processing of local and global visual information in humans and monkeys. The perception of the global and local attributes of visual forms has led to a large literature on humans. For example, Navon (1977) presented humans with large Roman letters made of smaller letters (e.g., an *H* made up with small *Hs* or Ss). Participants had to report the identity of the letter depicted at the global or local stimulus level. Navon (1977) observed that response times were shorter on average for the global letters. On the basis of these results and others, Navon (1977) argued that humans perceive the global structure prior to the local one.

Several experiments were conducted to comparatively assess this phenomenon (Fagot & Deruelle, 1997; Deruelle & Fagot, 1997b). These experiments used the joystick system described above. In a first phase of each trial, a compound stimulus similar to that used by Navon was briefly presented in the left or right visual field of the participants. In a second phase, two comparison forms appeared on the screen after sample stimulus presentation. One of these two forms matched the sample at either the global or the local level, and the other was different from the sample at both levels. Baboons and humans were tested in this task with the same compound stimuli. Results from humans agreed with those found by Navon (1977) and demonstrated shorter response times for global than for local trials. By contrast, baboons showed shorter response times in the case of the local trials. Thus, it appears that the two species processed the forms differently. It is interesting to note, however, that both baboons and humans had a similar pattern of lateralization. For the two species, a right-hemisphere advantage was found for global trials, and a reversed but not significant left-hemisphere advantage was observed for local trials.

To better understand the processing strategy adopted by each species, researchers in other experiments (Deruelle & Fagot, 1997a, 1997b) used a visual search task in which participants had to detect a target among a variable number of distractors. According to attentional theories (e.g., Treisman & Gelade, 1980), a linear increment of response times as a function of display size suggests that an attentional (serial) search procedure is used for target detection. By contrast, flat search slopes reveal the use of preattentive (i.e., automatic) detection procedures. The experiments used compound stimuli as both targets and distractors.

In each trial, there were 4, 8, or 12 stimuli on the screen. In some trials, the target differed from the sample at the global level only. In other trials, targets and distractors differed at the local level only. Un der both conditions, the participant had to move the joystick when the target was detected and to refrain from moving it when the target was absent. Flat search slopes were found in humans no matter what stimulus level they were to process (either global or local). In baboons, search slopes remained flat for the local trials, but, for the global trials, slopes linearly increased with display size. Thus, more attention is needed for the baboons than for humans to process the global targets. The fact that the two species showed the same right-hemisphere advantage for global processing (regardless of the amount of attention required for the task) suggests that lateralization in this task is rooted in early perceptual mechanisms.

The same joystick system as before was also used in a different theoretical context, with the aim of assessing lateralization for the processing of spatial relations in humans and baboons. The cerebral hemispheres of humans appear to be specialized to process spatial relations (Kosslyn, 1987). Studies involving normal and brain-damaged humans, or neural network simulations (see references in Kosslyn, 1994), converged to show a left-hemisphere superiority to categorize topological relations of the above or below type, and a right-hemisphere advantage to evaluate distances.

From an evolutionary standpoint, we questioned this left or right dissociation by using metric tasks. Indeed, nonhuman species are capable of processing distances (e.g., Fujita, 1997). However, to our knowledge, hem ispheric specialization in the processing of distances has not yet been investigated with nonhuman primates. In our study (Dépy, Fagot, & Vauclair, 1998), baboons and humans were tested with the divided-field procedure and were required to decide whether a dot was near or far from a horizontal line. Using an arbitrary matching-to-sample task, participants had to select a red stimulus when the sample belonged to the "near" category and a green one when it belonged to the "far" category.

Results of this experiment suggest a left-hemisphere advantage for categorical treatments and a right-hemisphere advantage for distance processing. Findings are thus consistent with the predictions derived from Kosslyn's (1987) model. First, naïve human participants exhibited a right-hemisphere advantage in the early trials of the task. Second, this effect disappeared with practice. It can be hypothesized from these results that in the early trials of the task, the metric aspects of the stimuli predominated and induced a right-hemisphere advantage. With practice, categorical aspects of the task increased and overrode the metric aspects, thus inducing a greater involvement of the left hemisphere.

A Primate Model of Hemispheric Specialization: Implications

The experiments described above elucidate the importance of the comparative approach for understanding human cognition and the evolution of hemispheric specialization. In general, the comparative approach questions the validity of human-based models of cognition. As the human cognitive system is the product of evolution, there must be continuities between humans and other primates. Fundamental bases of human cognition can thus be searched for in nonhuman primates. This inquiry has an advantage over a human-based approach. It avoids anthropocentric biases for building models of cognition and stresses their biological significance.

From another perspective, the search for cognitive similarities between humans and nonhuman primate species permits us to evaluate the dependence of the cognitive functions vis-à-vis the functions that are con sidered as being typically human, such as language. Studies with nonhuman primates illustrate perfectly the importance of the comparative approach for understanding human lateralization. Following Broca's (1861) first observation of a case of lateralization, there was a pervasive view that lateralization was a typical characteristic of humans (Geschwind & Galaburda, 1985). The results presented above clearly challenge that view by showing that lateralization is independent from language. Also interesting is that the study of animal lateralization showed important similarities between humans and other primates-for instance, in the processing of faces or in the treatment of the global or local characteristics of the visual forms. It is thus presumed that instead of being primarily linked to language, lateralization actually emerged as a solution to either perceptual or motor demands.

One additional concern may be raised with regard to the validity of a nonhuman primate model of lateralization. Given that the brain of nonhuman primates shares many structural and functional features with that of humans, the species consistencies and differences observed in hemispheric specialization should indicate whether lateralization in these species is homologous (i.e., the trait has a common phylogenetic origin) or analogous (i.e., the trait has evolved independently in the two species). The need to uncover the origin of a given trait calls for an adequate choice of the species to compare. In this respect, more studies of the. kind presented in this chapter should contribute significantly to solving this issue.

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