

**Specialized Processing of Primate Facial and Vocal Expressions: Evidence for
Cerebral Asymmetries**

Daniel J. Weiss, Asif A. Ghazanfar, Cory T. Miller & Marc D. Hauser*

Primate Cognitive Neuroscience Lab
Department of Psychology
33 Kirkland Street
Harvard University
Cambridge, MA 02138



*Correspondence should be addressed to:

Marc D. Hauser
Department of Psychology
33 Kirkland St., Rm 980
Harvard University
Cambridge, MA 02138
Phone: 617.496.7077
FAX: 617.496.7077
Email: hauser@wjh.harvard.edu

1. Introduction

In a recent review article, Michael Corballis (1998) states that perhaps “the major question confronting research on cerebral asymmetry is whether it will survive into the new millennium.” This volume certainly shows that the field has a strong basis, and that the contributions emerging from studies of animals are providing an increasingly precise picture of how cerebral asymmetries have evolved. Although the field has come a long way since the days when humans were considered uniquely lateralized, there are still many gaps in our knowledge. In this chapter, we attempt to fill in a portion of this gap, focusing explicitly on the nonhuman primates (hereafter, *primates*) and the specialized mechanisms underlying the production and perception of their facial and vocal expressions.

We begin our review by discussing the logic underlying the search for neural specializations, and then briefly discuss a selective set of problems associated with the comparative method. We then discuss current evidence for specialized processing mechanisms, focusing on the perception of faces and facial expressions, the perception of vocalizations, and the production of facial and vocal expressions. We conclude the chapter with a few comments on how future studies of hemispheric specialization must integrate behavioral studies of wild and captive animals with laboratory studies of neurophysiology.

1.1 *Why should we expect neural specializations?*

Like other species, including humans, it seems reasonable to expect primates to have a suite of specialized brain structures dedicated to processing ethologically-relevant behaviors. Thus, identification of species-typical behaviors, such as the production and perception of facial and vocal expressions, can guide explorations of species-specific neural mechanisms, or *specializations*. Neural specializations can manifest themselves in many ways, none of which are mutually exclusive. At the anatomical level, one may find left-right asymmetries in the sizes of surface features (sulci and gyri) or in the size and/or neurochemical composition of brains areas. Neurophysiological and experimental lesioning approaches can elucidate the functional role of the region in question, and this knowledge can guide the comparative study of behavioral and brain evolution (Cahmhi 1984; Konishi 1985; Allman, 1999; Ghazanfar and Hauser, 1999).

Using this pluralistic approach, neuroethological research has already added much to our understanding of how natural selection shapes brain-design for complex sensory behaviors (for reviews, see Hauser and Konishi, 1999) such as echolocation in bats (Kanwal, 1999; Simmons, 1971; Suga, 1989), song learning in birds (Marler, 1970; Nottebohm, 1999), and mate-choice in frogs (Ryan and Rand, 1999). For example, songbirds have species-typical songs which they use to attract mates and defend territories. The neural circuitry underlying this special behavior was identified (Nottebohm *et al.*, 1976) and demonstrated, via lesion and tracer studies, to be dedicated to the production and perception of song (for reviews, see Ball, 1999; Doupe & Solis, 1999; Nottebohm, 1999). In some species, the neural system for song has been shown to

be lateralized (Arnold and Bottjer, 1985), though the degree and direction of asymmetry varies between species, especially at the periphery (Suthers, 1997). Neurophysiological data reveal that neurons within song-related brain structures are extremely sensitive to the birds' own songs, but not to simple stimuli or songs from other individuals from the same species (Margoliash and Fortune, 1992; Doupe & Solis 1999).

1.2 The comparative method: some issues and problems

One of the central problems in comparative biology is to determine the evolutionary mechanisms underlying similarity between species. As evolutionary biologists have pointed out, however, there are two coarse-grained categories of similarity, and each provides deep insights into phylogenetic patterns and the history of selection pressures. On the one hand are *homologies*, characters that are shared between two species because of evolution by descent from a common ancestor. On the other hand are *homoplasies*, characters that independently evolved in different taxonomic groups due, quite often, to the process of convergence.

In general, studies of primates have often aimed their comparisons at humans, and this is particularly the case in the study of hemispheric specialization. When humans and primates show the same patterns or characters, it is often assumed that such similarities represent cases of homology. It is possible, however, that the similarity represents a case of homoplasy. Many cases of homology within the primates, especially at the behavioral level, have been defended on the basis of plausibility — specifically, that it is unlikely for the character to have evolved twice, once in each lineage. Although this is a reasonable argument to make for primates as a group, each case must be considered on its own. It is

certainly possible that some traits, shared in common between two species, evolved after the divergence point.

Although there are historical reasons for drawing comparisons between the patterns of hemispheric specialization obtained for humans, and those obtained for primates, there are two potential problems with this kind of focus. First, when neuroscientists look to animals for comparative data, they tend to draw classificatory boundaries with respect to higher order taxa such as “animal”, “vertebrate”, or “monkey”. Thus, several review papers on hemispheric specialization in humans present a cursory review of lateralization in “animals”, or sometimes “monkeys and birds.” As we will document below, there are often important differences between species, even within the same genus, and such differences are informative with respect to the selective pressures on brain organization. Second, studies of hemispheric specialization should also focus on similarities and differences between primates, independently of the patterns obtained for humans. This is important because it allows us to map patterns of primate brain evolution onto existing phylogenies that have used molecular, anatomical, behavioral and ecological characters.

In the literature reviewed below, it will be apparent to the reader that our understanding of the role of cerebral asymmetries in primate communication is restricted to only a handful of species. More specifically, though we know a great deal about asymmetries in hand use, and in coarse grained anatomy for a number of primate species, our knowledge of behavioral and neurophysiological asymmetries associated with the perception and production of communicative signals is largely restricted to *Macaca mulatta*, *Macaca fuscata*, and *Pan troglodytes*. As a result, our ability to draw inferences

about the patterns of evolution are minimal. Our goal, therefore, is to draw attention to what we know about the few species that have been studied, and hopefully inspire others to collect the relevant data on other species.

1.3 Why look for hemispheric asymmetries underlying the production and perception of communicative signals?

Much of what we know about hemispheric specialization in primates comes from the extensive studies conducted on the preferential use of the right or left hand or foot during grasping, reaching, and manipulating (see chapters 3 and 10, this volume). Considerably less is known about the extent to which primates show behavioral and neural asymmetries associated with the production and perception of species-typical, communicative signals. There are, however, a number of reasons to expect primates to show cerebral specializations for communicative signals. First, and as discussed in section 1.1, selection tends to favor specializations for interactions that are critical to survival and reproduction. For primates, vocalizations and facial expressions play a critical role in mediating social interactions critical to survival and mating. Thus, a wide variety of primates have vocalizations that indicate the presence of predators or the location of food, vocalizations that are used during mating and dominance-related social interactions, and facial expressions that are used to convey information about the probability of escape, attack, and friendly affiliation (Marler et al. 1992; Cheney & Seyfarth, 1990; Hauser, 1996; Preuschoft, 1995). Second, given the significant lateralization of human facial and vocal expressions, it seems likely that at least some

primates would show comparable asymmetries, at least for those expressions that they share in common (e.g., the “grimace” produced by humans and all primates).

We also would like to emphasize the importance of studying both perception and production. In Corballis’ (1999) review, he states that the strongest evidence of cerebral asymmetries in humans comes from studies of motor production as opposed to perception, and that there are two reasons to expect selection to have designed it in this way. First, there would be significant disadvantages to an asymmetric perceptual system since “a deficit on one side would leave an animal vulnerable to attack from that side, or unable to capitalize on prey that emerge on that flank” (p.g., 152-153). Second, asymmetries in motor production might well be advantageous, as when a task requires bimanual coordination, with each hand playing a different role. Although these are reasonable predictions, one can easily imagine advantages to a perceptual asymmetry (e.g., the barn owl’s asymmetric ruff which leads to advantages in sound localization and numerous other examples discussed in earlier chapters), and disadvantages to a motor asymmetry (e.g., vulnerability in defense against a competitor with opposite biases). Nonetheless, the observation that humans tend to show stronger directional biases for motor than perceptual systems is important to keep in mind in looking at the primate data (reviewed in Corballis, 1998).

Another reason why we need to consider both production and perception systems is that while some theories of communication have argued for co-evolutionary patterns, others have argued for a decoupling of these systems. For example, Ryan’s (Ryan et al. 1990; Ryan and Rand, 1995) work on the Tungara frog indicates that the female’s perceptual system acts as an evolutionary pressure on the male’s production system.

Specifically, because the tuning of the female's auditory system is for frequencies that are lower than the male's advertisement call, females show preferences for synthetic calls that fall outside the range of species-typical variation. As such, female choice acts as a selective pressure on the evolution of the male's character. Although studies of primate communication are not yet in the position to look at the evolution of production and perception systems, by discussing what is currently known about cerebral asymmetries for communicative expression and perception, we will begin to lay the groundwork for this important problem.

2. Specialized processing of faces: perceptual mechanisms

Faces represent a complex class of stimuli. They have highly invariant features such as the T-configuration formed by the eyes, nose, and mouth, as well as variable features such as interocular distance, nose shape, and so forth. In addition, faces convey many important types of information including sex, identity, and emotional state. Given that the visual identification and recognition of individuals and their facial expressions is an important component of the behavioral repertoire of at least some primates species, it is of interest to investigate whether other species besides *Homo sapiens* have specialized neural mechanisms for face processing.

2.1 The inversion effect

One source of behavioral evidence supporting the notion of specialized face processing is the inversion effect. For humans, face processing is significantly affected

by orientation. When subjects are presented with an inverted face, they are impaired in recognition tasks, showing both a decrease in accuracy and slower reaction times (Yin 1969, 1970). This phenomena may be even more robust for unfamiliar faces (e.g., other-race faces; Valentine and Bruce, 1986a). This effect seems particularly strong for faces as opposed to non-face visual objects, and has been used to argue for a specialized, even modular, processing mechanism (e.g., Farah et al., 1995; Kanwisher et al., 1998). Several researchers have concluded that subjects actually encode upright faces holistically while inverted faces are encoded in a piecemeal fashion (Yin, 1969, 1970; Carey and Diamond 1977; Bruce and Humphreys, 1994). To that effect, an inversion effect may be found for some nonface objects, such as dot configurations, provided that they are configured to be processed holistically (Farah et al., 1995). It has been posited that the neural mechanisms for face processing in humans have been designed to handle the configuration of upright faces (e.g., Perrett, 1988) and these mechanisms reside primarily in the right hemisphere (see Section 3). Furthermore, the right hemisphere bias for face recognition disappears when an inverted face is presented (Leehey et al., 1978). Therefore, the inversion effect may provide a good behavioral test for finding evidence of specialized face processing in primates.

The majority of experiments on the inversion effect have been carried out with macaques (*Macaca*). An early study by Bruce (1982) with rhesus macaques failed to find an inversion effect. Bruce concluded that macaques lack the orientation-dependent face recognition mechanism that, in humans, matures within the right hemisphere. More specifically, he suggested that macaques may not develop a configurational mechanism for face recognition because they mature at a much quicker rate than human infants (the

supposition being that early developmental experience with faces may shape the configurational mechanism). Further, he suggested that macaques have minimal hemispheric specialization for any function. However, these suggestions must be reexamined in light of more recent studies (detailed below).

In a series of well-designed behavioral and neurophysiological experiments, Perrett and colleagues (1988) re-examined the claim that monkeys process faces in a different manner from humans, focusing in particular on the failure to find an inversion effect. Initially, the macaques were trained to distinguish between faces (human and macaque) and common objects (including human and macaque non-face body parts). To ensure that subjects were actually seeing the images as faces, the experimenters trained the monkeys to generalize to novel faces (in the face versus common object discrimination condition). Following this generalization phase, the stimuli were presented upright or inverted. The subjects showed no difference in reaction time for correctly identifying the face images, thus providing no evidence for an inversion effect. Based on these results, Perrett and colleagues hypothesized that the monkeys were performing the face-non-face discrimination on the basis of distinctive facial features (e.g., the eyes alone) as opposed to the configuration of features. Thus, if a subject identified a salient facial feature then it would press the “face” button irrespective of how many other facial features were present or how they were configured.

To address this possibility, Perrett and colleagues (1988) postulated that it might be possible for primates to learn a discrimination between faces and non-faces on the basis of configuration, and then, on a subsequent test, show an inversion effect for the face category. This is a reasonable hypothesis given that for humans, the inversion effect

appears to result from processing upright faces on the basis of configuration and inverted faces on the basis of distinctive features. A second experiment was designed to test this hypothesis with rhesus macaques.

Rhesus macaques were taught to discriminate sets of human and macaque faces from scrambled face images where all the features were present, but not in their proper position. The monkeys were then trained on horizontal stimuli, followed by training on inverted stimuli. To test for an inversion effect, Perrett and colleagues presented the original training stimuli in four orientations (0° , 90° , 180° , 270°), and then retrained the subjects on another face using the same procedure. Under these conditions, the macaques took longer to respond to both horizontal and inverted orientations compared with the upright orientation. This effect was replicated with a second set of novel face stimuli. Perrett and colleagues concluded that rhesus process faces in a similar fashion to humans. Prior failures to find an inversion effect in primates may have been due to a lack of constraints on processing strategies. In particular, without training subjects to attend to configuration, alternative features may be used to solve the task, resulting in a misguided understanding of the potential mechanisms underlying face processing in primates.

Despite the findings of Perrett and colleagues, there have been more recent studies that have failed to find an inversion effect for conspecific faces in rhesus macaques. A study by Wright and Roberts (1996) showed that rhesus monkeys appear to respond differently to human faces as opposed to the faces of Great Apes, Old and New World monkeys, and prosimians. Their study compared human and rhesus monkey subjects, finding that both species showed inversion effects for human faces, but not for

the other primate faces, and not for scenes. This finding is difficult to interpret in light of Perrett et al.'s (1988) finding.

A recent study by Parr and colleagues (1999) also challenges the hypothesis that the inversion effect found in primates is specific to faces. They suggest that rhesus monkeys may show inversion effects for a number of classes of stimuli, not only faces. Using a match-to-sample procedure, Parr and colleagues tested rhesus monkeys with conspecific and heterospecific faces (including humans and primates), as well as automobiles and abstract shapes. They found evidence for an inversion effect with conspecific faces, capuchin (*Cebus apella*) faces, and automobiles. In contrast to previous studies, they failed to find evidence for an inversion effect with human faces, as well as for abstract shapes. Thus, Parr and colleagues concluded that the inversion effect in rhesus monkeys is not face-specific and that previous studies of this effect do not provide valid evidence for a specialized face-processing mechanism in this species. These findings are also difficult to reconcile with previous studies.

Taken together, current evidence suggests that, under certain conditions, rhesus monkeys show an inversion effect for human and conspecific faces (see Section 2.2). To observe this effect, however, rhesus must be constrained to use configurational cues, forcing them to process faces in the same manner as humans. In addition, it is important to have a generalization task to ensure that the subjects are actually processing face images as faces. Those studies that have failed to find an inversion effect have generally failed to provide evidence that their subjects were responding to configuration as opposed to distinctive features, and thus, failed to show that subjects were responding to faces as “faces”.

While there have been numerous studies of face processing in macaques, research on the Great Apes has been limited, with all efforts focused on chimpanzees (*Pan troglodytes*). Tomonaga and colleagues (1993) studied the inversion effect in a chimpanzee with a long history of formal experimental training (Matsuzawa, 1996). The central goal of this experiment was to assess whether chimpanzees process heterospecific faces (humans) differently from the way in which they process conspecific faces. Subjects (4 humans and one chimpanzee) sat at a panel with six buttons, each one corresponding to a different face (there were 6 faces total, 3 human and 3 chimpanzee). The subjects were trained to press the button corresponding to the presented face. The training stimuli consisted of upright faces. Test conditions involved presentation of rotated (horizontal) and inverted faces. The chimpanzee had more difficulty in identifying the horizontal faces but did not show a significant inversion effect for faces (as measured by reaction time data). In a more recent study by Parr, Hopkins, and de Waal (1996), however, the inversion effect was found in four out of five chimpanzees when they were presented with unfamiliar conspecific faces. In a control, using abstract shapes, two out of five subjects showed better performance for upright orientations. Thus, there was some evidence for an inversion effect to conspecific faces, but this effect was not restricted to faces; this result parallels the findings of Parr and colleagues (1999) on rhesus macaques.

Parr, Dove and Hopkins (1998) tested five chimpanzees on their ability to discriminate human, chimpanzee, and capuchin faces, as well as automobiles, in both upright and inverted orientations. All subjects performed better on upright than inverted stimuli, across all conditions. However, a statistically significant difference in

performance was only obtained on upright versus inverted presentations of chimpanzee and human faces, and not for capuchin faces and automobiles.

Chimpanzees represent the only Great Ape tested to date, and thus, nothing can be said about face processing in bonobos, gorillas, and orangutans. In parallel with studies of rhesus monkeys and humans, however, most studies of chimpanzees reveal evidence of an inversion effect to human and conspecific faces, providing support for a specialized processing mechanism (see Section 2.2).

In contrast to the other primates, relatively few studies have investigated face processing, and especially the inversion effect in New World monkeys. Phelps and Roberts (1994) studied face processing and the inversion effect in squirrel monkeys, and contrasted their performance with humans and pigeons. In the initial experiment, both humans and one squirrel monkey showed inversion effects for human faces. However, neither showed significant inversion effects for monkey faces (a category comprised of many different species). A follow up experiment showed that a different squirrel monkey showed better reference memory for upright as opposed to inverted human and Great Ape faces, but not for Old and New World monkey faces, prosimian faces or scenes. The pigeons showed no inversion effect at all.

Weiss and Kralik (in press) recently completed a study of face processing in cotton-top tamarins, using a procedure that closely matched the second experiment of Perrett et al. (1988). In the initial stages of the experiment, four subjects were trained to discriminate two human faces from two scrambled human faces. After this training, none of the subjects showed an inversion effect. As previously discussed, however, this experiment does not provide a fair test of the inversion effect because there was no

evidence that the tamarins were using configuration to classify the stimuli as faces. In fact, more detailed analyses revealed that the tamarins were attending to distinctive features such as the presence or absence of an eye in a particular location, and then using these to make an appropriate response. In a second condition, one subject was trained to focus on the configuration of the face, and was then tested on a series of generalization trials involving novel faces. Under these conditions, there was no evidence of an inversion effect based on either classification accuracy or reaction time.

The data from New World monkeys is extremely limited, both in terms of the number of species and number of individuals tested. Squirrel monkeys appear to show an inversion effect for human and Great Ape faces, while cotton-top tamarins fail to show an inversion effect for human faces. There is no evidence that any New World monkey shows an inversion effect to Old World monkey, prosimian or conspecific faces, suggesting that these faces may be processed differently than Great Ape and human faces.

Patterns and problems

Studies of several primate species report evidence of an inversion effect for faces. Such results support the claim that both humans and primates have evolved a specialized mechanism for face processing. Overall, however, the literature on inversion effects in primates is difficult to interpret. Even within the same species, there are conflicting patterns as to the presence of an inversion effect: with rhesus monkeys, Perrett and colleagues (1988) found an inversion effect whereas Wright and Roberts (1996) did not. It is possible, however, that the apparent inconsistencies are due to methodological differences between studies. We consider six possibilities. Although there have been no

studies that directly test the effects of these methodological differences, we suggest that these factors may have a substantial impact on experimental findings.

First, some studies have used a match-to-sample task (e.g., Parr et al., 1999) , while others have used either a discrimination (e.g., Perrett et al., 1988) or preferential looking task (Tomonaga, 1994). These techniques are associated with different task demands that may well affect how stimuli are processed. An additional methodological note is that the body posture of the test subjects may influence the results. Specifically, some species may use head cocking (e.g., tamarins) or other strategies in order to view faces in a different orientation than those presented by experimenters.

Second, few studies have verified that subjects were attending to the configuration of facial stimuli when selecting an appropriate response. More specifically, only two experiments (Perrett et al, 1988; Weiss and Kralik, in press) have provided evidence that subjects used the configuration of facial features in choosing between responses or stimuli. As studies of humans have illustrated, because the configuration of a face is critical to its categorical status as a “face”, studies of face processing in primates must first show that their subjects are attending to configuration before testing for specialized processing mechanisms.

Third, some experiments report reaction time differences (e.g., Perrett et al. 1988; Weiss & Kralik in press), while others report only accuracy scores (e.g., Parr et al., 1999). In most tests of face processing that have been conducted on humans, the inversion effect is subtle and requires statistical testing of reaction time data to find the effect. This may explain why some studies of rhesus macaques do not find inversion effects (e.g., Bruce, 1982) while other studies do (Perrett et al., 1988).

Fourth, there are significant differences in the kinds of stimuli presented across experiments. Some experiments limit the stimuli to faces while others include additional body parts, as well as inanimate objects. Further, some contrast responses to conspecific as opposed to heterospecific faces, whereas others contrast conspecific faces with non-face objects. In our opinion, tests of specialized face processing should include a generalization phase showing that subjects can appropriately respond to novel faces. In addition, comparing subjects' performance with face stimuli to performance with other stimulus types may determine whether the effects are particular to a face processing mechanism.

Fifth, almost all studies of face processing in primates are based on small sample sizes. Rarely do studies of the face inversion effect exceed one or two subjects. This greatly limits our ability to draw inferences about phylogenetic patterns.

Despite the limitations we have sketched above, it is reasonable to assert that in studies that are conducted with appropriate measures (i.e., tests to determine that subjects are using configuration in processing images and can generalize from the original training set, accuracy and reaction time measures) we can be confident that the results are comparable to human results and thus provide evidence for specialized processing for faces.

2.2 Hemispheric specialization and face perception

In humans, evidence from both clinical and experimental studies have shown that face processing mechanisms are lateralized predominantly (although not entirely) to the

right cerebral hemisphere. Patients with brain damage in the right cerebral hemisphere are often more impaired on tasks involving face perception than patients with similar damage in the left hemisphere. Experimental studies have shown that presentation of faces to the right hemisphere (through the left visual field) leads to faster processing than presentation to the left hemisphere (Hilliard, 1973, Whitman and Keegan, 1991, Burton and Levy, 1991).

The earliest studies with primates failed to find any evidence of hemispheric asymmetries in processing faces (e.g., Overman and Doty, 1982; Hamilton and Vermeire, 1983). More recent experiments suggest, however, that primates also show a right hemisphere bias for processing faces. In a study of split-brain rhesus macaques, Hamilton and Vermeire (1983, 1988) reported a right hemisphere advantage for discriminating individual animals by face and by facial expression. The stimuli consisted of rhesus monkey faces. Specifically, subjects were required to distinguish between slides of different individuals and slides of the same individuals producing different facial expressions. Of the split-brain monkeys tested, 70% showed a right hemisphere advantage based on accuracy scores. Vermeire and Hamilton (1988) then ran this experiment again, but contrasted performance of split-brain monkeys on upright versus inverted faces. Although a right hemisphere advantage was found for upright faces, the cerebral asymmetry disappeared for inverted faces. In addition, there was enhanced right hemisphere performance on both retention and generalization tasks performed 6 months after the conclusion of the aforementioned experiment (Hamilton and Vermeire, 1991).

Morris and Hopkins (1993) used a visual half-field presentation approach to determine whether captive chimpanzees show an asymmetry in processing human

chimeric facial stimuli. Three chimpanzees were trained to discriminate normal “happy” faces from normal neutral faces. Once criterion was reached (85% correct), subjects had to discriminate chimeric faces in which half of the facial stimulus was smiling and half was neutral. Analyses of classification accuracy indicated that the subjects demonstrated a significant left hemispatial-field advantage, and thus, a right hemisphere advantage for processing faces.

Patterns and problems

Hamilton and Vermeire’s results (1991) support the hypothesis that upright faces are processed preferentially in the right hemisphere and that this processing difference is what drives the inversion effect. One drawback of this work, however, is that no reaction time data are reported. Thus, although the accuracy scores for the inverted faces may have been similar across hemispheres, there may have been a difference in reaction time.

In summary, studies to date provide evidence of a specialized mechanism for face processing in primates. The primary evidence, mostly from studies of macaques, reveals an inversion effect in both intact (e.g., Perrett et al., 1988) and split-brain subjects (Hamilton and Vermeire, 1991). Moreover, these studies suggest that the right hemisphere plays a dominant role in face processing, and in particular, in processing upright faces (Hamilton and Vermeire, 1991).

In the future, behavioral experiments must focus on the Great Apes and the New World monkeys in order to determine whether the patterns obtained for rhesus macaques are consistent across the primates or differ as a function of socioecological pressures. Such comparative work, which depends critically on the use of comparable methods and

standards of evaluation, is likely to shed light on the evolutionary history of the hemispheric bias for processing upright faces in the right hemisphere. For example, do more arboreal species, who may depend less on visual features for species and individual recognition, fail to show evidence of a specialization for faces? Do species that spend considerable amounts of time in inverted positions, fail to show an inversion effect due to their species-typical locomotory experiences? Likewise, do some species attempt to view inverted faces in the upright position by cocking their heads? In cases where upright and inverted faces are processed equivalently (i.e., no accuracy or reaction time differences), do they nonetheless show a hemispheric bias for processing faces at the neuronal level?

3. The neural basis of face perception

3.1 Face-selective neurons in the temporal cortex of macaques

Cognitive studies, both clinical and experimental, of face perception by humans suggest that face and object recognition involve qualitatively different processes that occur in different brain regions (Damasio *et al.*, 1990). The results of these studies suggest that face processing by humans is a behavior that requires specialized neural mechanisms. This hypothesis has been borne out by studies using patients with lesions and functional imaging of normal subjects which show that there are discrete regions of the brain which are essential to the recognition of facial identity and expression (Damasio *et al.*, 1990; Haxby *et al.*, 1999; Kanwisher *et al.*, 1997; Puce *et al.*, 1996; Puce *et al.*, 1999). Many of these studies also show a lateralization of face processing to the right hemisphere. There is also evidence suggesting that primates may have homologous neural mechanisms for face processing (reviewed in Rolls, 1999).

Bruce, Desimone, and Gross (Bruce *et al.*, 1981; Desimone *et al.*, 1984) published the first exhaustive descriptions of ‘face’ cells in the neocortex of macaque monkeys, and the existence of such cells has been confirmed by subsequent studies from several laboratories. The unique property of these neurons is that they respond selectively to the presentation of faces. That is, while they may respond to other complex visual stimuli, these neurons respond much more rigorously (at least double the magnitude) to faces or components of faces (such as eyes or mouths) than to other stimuli. Face cells are primarily found in the temporal cortex, specifically in the inferior temporal (IT) cortical area, TE (Desimone *et al.*, 1984; Hasselmo *et al.*, 1989), and in the superior temporal sulcus (STS) (Bruce *et al.*, 1981; Hasselmo *et al.*, 1989; Perrett *et al.*, 1982). These regions are homologous with regions in the human temporal lobe which are activated by faces or facial expressions (Kanwisher *et al.*, 1997; Puce *et al.*, 1999).

3.2 Gaze direction and face cells

Among social species of primates (including humans), the ability to detect where another individual is looking is highly adaptive because the gaze direction of an individual can be used to predict that individual’s movements or actions. In support of this, studies on rhesus monkeys have shown that when viewing faces, conspecific or otherwise, individuals selectively attend to the eyes when compared to other features of the face (Keating and Keating, 1982; Nahm *et al.*, 1997; Wilson and Goldman-Rakic, 1994). In these studies, selective attention was measured by tracking eye movements while the subjects freely viewed visual stimuli and recording the duration and location of visual fixation points. There is also evidence that primates can attend to another

individual's direction of gaze, using a combination of head and eye cues (Povinelli and Eddy, 1996; Tomasello et al., 1998; Santos and Hauser, 1999).

To investigate the neural bases for the perception of gaze following, Perrett and his co-workers (1985) searched for neurons in the temporal cortex that may respond to such cues. They reasoned that since neurons in the STS are often tuned to many views of the head (face, both profiles, and the back of the head)—more views than are needed for recognition purposes—that these neurons may play a role in coding social intention. In other words, these cells may signal where another individual is attending by encoding the combination of head orientation and gaze direction. Indeed, Perrett et al. (1985) found that many of the cells responsive to head view were found to be equally (if not more) sensitive to gaze direction. The most robust responses could be elicited from these cells if head orientation and gaze direction in the stimuli were matched; that is, if the cell was selective for a head turned laterally away from the monkey (to the right, for example), then that cell gave a greater response to the stimulus if the eyes were also laterally-oriented (eyes looking to the right). This finding is also supported by lesion experiments. Monkeys trained to follow eye gaze direction showed significant deficits following bilateral lesions of the STS (Campbell *et al.*, 1990), but no deficits for face recognition in general (Heywood and Cowey, 1992).

3.3 Cellular correlates of hemispheric specialization for faces in macaques

In the only study of its kind, Perrett et al. (1988) compared single unit physiology data with results from a modified version of an upright versus inverted face discrimination task to address the question of specialized processing of faces in monkeys.

Reaction time measurements showed that monkeys were able to discriminate upright configurations of faces significantly faster than stimuli presented in the horizontal or inverted orientations. This result is nearly identical to those based on humans performing the same task. Moreover, the monkeys' reaction time data corresponded nicely with the single unit data. Thus, while many face-selective cells respond with a similar magnitude to either upright or inverted faces, the onset latency (or how quickly the neuron responds) differs. A majority of face-selective neurons respond with a shorter onset latency to upright faces when compared to responses to inverted faces (Perrett *et al.*, 1988).

To determine whether the distribution of face cells is lateralized in macaques, Perrett *et al.* (1988) quantified the number of face-selective neurons encountered in the STS of both the left and right hemisphere using a within-subjects design. Surprisingly, for the three monkeys tested, there was a greater probability of encountering face neurons in the *left* hemisphere than in the right.

3.4 Neural encoding of facial identity and expressions

For humans, there appear to be separate mechanisms for processing facial identity and facial expressions. For example, prosopagnosics have difficulty identifying individuals by their faces, but have no difficulty in categorizing facial expressions in general (Damasio *et al.*, 1990). In normal subjects, reaction times are faster for matching identity for familiar versus unfamiliar faces, while the use of familiar versus unfamiliar has no effect on reactions times for matching facial expressions (Bruce and Young, 1986). A similar dissociation for identity and expression discrimination has not been directly observed in monkeys tested on behavioral tasks.

In contrast to studies using behavioral assays, neurophysiological experiments suggest that macaques may have different systems for processing facial identity and expression. Hasselmo et al. (1989) recorded from cells in the temporal cortex to determine whether facial identity and facial expression are encoded by the same or different populations of neurons in rhesus macaques. In their experiments, the faces of three macaques with three different expressions were used as stimuli and the neural responses measured and compared across identities and expressions. The expressions used were a calm/neutral face, a slightly open-mouth threat, and a full open-mouth threat. Neurons were sampled from the IT cortex and the STS. Two significant findings emerged from this study: 1) some neurons responded selectively to different identities independent of facial expression, while other neurons responded selectively to specific facial expressions independently of facial identity; and 2) neurons sensitive to facial identity were located in the IT cortex, while neurons sensitive to facial expressions were found primarily in the STS. The difference in anatomical distribution was statistically significant.

Studies of normal humans using neuroimaging techniques, as well as studies of patient populations with focal lesions in the temporal lobe, support the notion that there are different pathways for processing facial identity and facial expression (Adolphs *et al.*, 1996); Kanwisher *et al.*, 1997; Puce *et al.*, 1999). Thus, taken together these results suggest that the similarity in face processing mechanisms between humans and macaques is a case of homology; this claim holds even if macaques, or other primates, fail to show evidence of cerebral asymmetry.

Patterns and problems

The finding of left-hemisphere bias for distribution of face-selective cells in the STS (Perrett *et al.*, 1988) stands in contrast to the split-brain studies on macaques, the visual-half-field study of chimpanzees (see section 2.1 and 2.2) and the human imaging data, where there is greater activation of the STS in the *right* hemisphere than in the left for face stimuli (Puce *et al.*, 1999). Perrett and colleagues are the only group to study this issue using electrophysiological methods, and, unfortunately, their subject group consisted of only three monkeys. Furthermore, there is the issue of sampling bias. As stated by the authors, in two of the monkeys, the STS of the left hemisphere was sampled more extensively than that of the right hemisphere (Perrett *et al.*, 1988). Nevertheless, a recent human imaging study demonstrates that when subjects are required to attend to the eye gaze of face stimuli, the *left* STS is more active than the right (Hoffman and Haxby, 2000)—a finding which lends some support to the finding of Perrett and colleagues. In the future, it will be important for studies to track the eye movements of subjects (see below). Ultimately, the question of cerebral asymmetries for face processing in primates may best be addressed by techniques with greater spatial resolution, such as fMRI (Logothetis *et al.*, 1999).

Considering the neural segregation of face recognition versus expression in primates, several caveats must be considered. One potential problem concerns the limited number of ‘expressive’ stimuli used. Only three expressions were used, one of which was a ‘calm/neutral’ face. The other two were open mouth threats of different magnitudes. Macaques have a suite of distinctive facial expressions, of which the open mouth threat is only one exemplar among several associated with negative/withdrawal

emotions (Hauser, 1993, 1999; Hauser & Akre, in prep; Hauser et al. in prep). Thus, these experiments may not have robustly tested the selectivity of temporal lobe neurons for facial expressions.

Many primates, including macaques, preferentially look at the eyes when viewing other monkey faces (Keating and Keating, 1982; Nahm *et al.*, 1997; Wilson and Goldman-Rakic, 1994), and the eyes remain the primary targets for visual scanning for a range of facial expressions, including open-mouth threats, lipsmacks, yawns and fear grimaces (Nahm *et al.*, 1997). However, for some expressions, such as lipsmacks and yawns, there were no significant differences between the average time spent looking at the eyes versus the mouth, but for other expressions, such as the open-mouth threat and the fear grimace, significantly more time was spent looking at the eyes (Nahm *et al.*, 1997). Thus, it would be of interest to know what facial features the ‘expression-selective’ neurons are coding. Is it the mouth, the eyes, or a combination of both? Also, how are the responses of neurons modulated by vocal expressions in which both visual and auditory cues are present? This is an interesting problem given the fact that human infants preferentially attend to the eyes of faces, whether the face is still or talking (Haith *et al.*, 1977), and infants are clearly sensitive to both visual and auditory information (Kuhl and Meltzoff, 1982). Future research on the neurophysiology of facial expression must explore the possibility of different responses, based in part on such factors as emotional valence (e.g., positive/approach versus negative/withdrawal), whether or not the eyes are directed at the receiver or away from him, and whether the individual giving the expression is familiar or unfamiliar.

4. Specialized processing of vocalizations: perceptual mechanisms

4.1 Specialization in vocal perception

The task of vocal perception involves extremely complex processing. The first challenge facing the receiver is to detect the vocalization despite environmental noise and attenuation. Once the signal is detected, the receiver must then classify the type of vocalization and the source. Successful classification requires the receiver to attend to the relevant acoustic parameters, both spectral and temporal. In humans, for example, temporal cues such as duration, interval, and order of acoustic features are important for speech perception and sound categorization (Harnad, 1987, Liberman et al., 1967). In fact, data from language-impaired children have contributed to the theory that speech perception is based on rapid processing of temporal information (Tallal et al., 1993). Given that vocal classification and communication is an important component of the behavioral repertoire of most primates species, it is of interest to investigate whether other species besides *Homo sapiens* have specialized neural mechanisms for vocal perception, and whether such mechanisms are lateralized.

To determine whether primates might exhibit similar specializations for processing their own vocalizations, psychophysical experiments were conducted on Japanese macaques (*Macaca fuscata*), focusing on two functionally distinctive variants of the “coo” call (Beecher, et al., 1979, Zoloth, et al., 1979). These vocalizations, referred to as the smooth early (SE) and smooth late (SH) high coos, differed in the relative temporal position of the peak frequency, as well as the social context in which they were given (Green, 1975). Experiments were designed to assess whether Japanese macaques,

compared to closely related species (pig-tailed macaques, bonnet macaques, and vervet monkeys) have evolved specialized mechanisms for classifying conspecific vocalizations as a function of distinctive acoustic features. Two conditions were tested. In condition one, subjects were required to discriminate calls based on the position of the peak frequency of the fundamental. In condition two, discrimination was based on the initial frequency of the fundamental. While comparison species were better able to distinguish the vocalizations using the initial frequency, only Japanese macaques performed better at the task of distinguishing calls based on the peak frequency. Thus, the findings from these experiments, as well as subsequent studies (May et al., 1988), are consistent with the interpretation that Japanese macaques have evolved specialized mechanisms to distinguish between their call types. What these studies leave open is whether such specializations are largely innate as opposed to shared by experience with a particular vocal repertoire, and whether the pattern obtained for coos would obtain for other call types within the repertoire.

4.2 Behavioral asymmetries in vocal perception

The left hemisphere is thought to be dominant for the more formal aspects of language processing (such as syntax, semantics etc.) while the right hemisphere appears dominant for processing the paralinguistic or prosodic cues (e.g., rhythm, melody). Evidence for cerebral asymmetries underlying language processing come from cases of brain damaged patients, dichotic listening studies, and recent neuroimaging work (e.g., Price, 1998, Mueller et al., 1999).

Petersen and colleagues (1978,1979) conducted a series of experiments to test whether Japanese macaques, thought to have evolved specialized mechanisms to distinguish between their call types, exhibit behavioral asymmetries in processing conspecific vocalizations. In their initial study (Petersen et al., 1978), they trained Japanese macaques to discriminate among several natural exemplars of two functionally distinctive, tonal vocalizations (the coos mentioned in section 4.1). The stimuli were presented monaurally, alternating between ears, and the performance for each ear was compared. They found that the Japanese macaques performed better when the stimuli were presented to the right ear (and thus left hemisphere). Several other primate species (bonnet and pig-tailed macaques and vervets) were also tested, but only one (vervet) showed a significant ear advantage, and in the same direction as Japanese macaques. Follow up studies showed that all species attended to the same acoustic features of the call. Petersen and colleagues therefore concluded that the communicative valence of the calls for Japanese macaques was responsible for the enhanced left hemisphere performance. Consequently, the pattern observed among Japanese macaques appears to resemble the left hemisphere bias for language processing in humans.

Although the work on Japanese macaques represents a landmark in the field, several questions remain. First, because the experiments focused exclusively on coos, it is not yet known whether the enhanced right ear performance would generalize to other vocalizations within the repertoire. Second, because one vervet monkey showed the same pattern as the Japanese macaques, the extent to which the right ear bias represents a species-specific specialization remains unclear. Finally, it is unclear whether the right ear

bias would be observed under more naturalistic conditions, and in young as well as older individuals.

To address some of these issues, Hauser and colleagues conducted a series of field experiments with both adult and infant (4-12 month olds) rhesus monkeys (*Macaca mulatta*) living on the island of Cayo Santiago, Puerto Rico. In the first experiment (Hauser and Andersson, 1994), a speaker was concealed in vegetation 180° behind the target subject, 10-12 m behind one side of a chow dispenser. When the subject's back completely faced the speaker, and the camera was lined up with both the speaker and subject, the playback was initiated and the subject's head orienting response recorded onto video. Recording the response onto video allowed for an unambiguous assessment as to which direction the subject turned to listen. Three responses were possible: turn right, turn left, or no detectable response.

The experimental stimuli consisted of exemplars from twelve call types that could be separated into three broad categories: aggressive, fearful, and affiliative. The underlying assumption of the experiment was that if the subject turned its right ear toward the speaker, then the acoustic input would be biased toward the left hemisphere of the brain; though both hemispheres would receive input, the input to the left hemisphere would have greater intensity. Likewise, if the subject turned its left ear toward the speaker, then the input would be biased to the right hemisphere of the brain. As a control stimulus, Hauser and Andersson played the alarm call of the ruddy turnstone (*Arenaria interpres*), a seabird that lives on Cayo Santiago. The turnstone's alarm call is familiar to the monkeys and may have significance in alerting the monkeys to the presence of humans.

Results showed that adult subjects turned with the right ear leading (left hemisphere) in response to conspecific vocalizations, but turned with the left ear leading in response to the ruddy turnstone's call. In contrast, infants failed to show a significant head orienting bias for either the conspecific or the ruddy turnstone calls. At present, the mechanisms underlying these age differences are not well understood. One possibility is that hemispheric differentiation develops only when the vocalizations acquire meaning (possibly occurring up to two years of age; see Cheney and Seyfarth, 1990; Gouzoules & Gouzoules 1989). A second possibility is simply that complete maturation of the hemispheres requires at least one year to complete. As a result, the orienting response of the infants is based on general rather than selective acoustic processing mechanisms. More research is needed to determine when rhesus monkeys acquire adult-levels of comprehension and when the hemispheric asymmetries observed in adults become fully mature. Nevertheless, the overall results from this experiment provide strong evidence for the existence of a left hemisphere bias for processing conspecific vocalizations in the adult rhesus macaque. These findings parallel the results obtained for Japanese macaques as well as for humans tested in dichotic listening experiments (e.g., Bryden, 1982).

In humans, the magnitude of the lateralization effect can be altered by speeding up or slowing down formant transitions within a syllable (Schwartz and Tallal, 1980). In order to test whether rhesus macaques are similarly affected by temporal manipulations, a follow-up series of investigations have been undertaken to determine which acoustic features of the vocalizations are responsible for the head turning preference, and thus, the presumed hemispheric bias. The first series of experiments (Hauser et al., 1998) looked at the temporal features of three different pulsatile call types: a grunt (affiliative signal

involving food or conspecific), a shrill bark (alarm signal), and a copulation scream (mating signal). These calls were chosen because of the available acoustic analyses and studies on call context (e.g., Bercovitch et al. 1995; Hauser 1993; Hauser and Marler, 1993a). The signals were presented in both manipulated and unmanipulated form. The manipulated calls consisted of 1) a reduction of the interpulse interval (IPI) to zero or the population minimum and, 2) an expansion of the interpulse interval to the population maximum or twice the population maximum. The main prediction for this experiment was that calls manipulated beyond the species-typical range should elicit a different pattern of head orientation than what had been reported for unmanipulated conspecific calls (Hauser and Andersson, 1994). Results showed that when the IPI was eliminated from the grunts and shrill barks, there was no significant orienting bias. In contrast, the right ear bias was preserved when this manipulation was imposed on the copulation calls. When the IPI was extended to the maximum in the population, there was a tendency for subjects to orient with the left ear leading for both grunts and shrill barks, but this bias was not statistically significant; for copulation calls, the right ear bias was preserved. When IPIs were increased to twice the population maximum, subjects consistently turned left for grunts and shrill barks, but again maintained a right ear bias for copulation calls.

Overall, results from experiments on grunts and shrill barks support the hypothesis that manipulations of the IPI beyond the species-typical range of variation cause a shift from a right ear bias to either no bias (with the IPI eliminated) or to a significant left ear bias (with the IPI stretched to twice the population maximum). This pattern of response was not, however, observed for playbacks of copulation screams. The acoustic morphology of the copulation scream may provide insights into why the

temporal manipulations imposed failed to elicit a change in the direction of head orientation. Grunts and shrill barks are produced with a minimum of two pulses, while copulation screams can be produced with either one or many pulses. Consequently, whereas the IPI appears relevant for classifying grunts and shrill barks, it may not be relevant for copulation screams, at least in terms of assessing whether it is or is not a conspecific signal; the inter-pulse interval of copulation screams may, however, be relevant to male quality (e.g., Hauser, 1993).

More recent work, using the same head orienting procedure, has focused on a different acoustic manipulation: reversing the call (Ghazanfar & Hauser, in prep). This type of manipulation preserves all of the spectral energy in the call while inverting the temporal relationships. For this experiment, our goal was to assess the perceptual salience of a time-reversed amplitude envelope. Specifically, we tested the hypothesis that if rhesus monkeys use the amplitude envelope of a signal to classify it as falling within or outside the category of “conspecific”, then reversing a call should eliminate the head turning bias observed in the original experiments involving unmanipulated calls.

The calls used in this experiment included two aggressive calls (bark, pant threat), one food call (harmonic arch), and one alarm call (shrill bark); each of these calls was used in the original Hauser and Andersson (1994) study. The aggressive calls are characterized by a symmetrical amplitude envelope, and thus reversing the signal has only a minimal effect. In contrast, both the food and alarm calls have asymmetric amplitude envelopes, and thus reversing the signal should have a more noticeable effect. To human observers who have had experience with the rhesus repertoire, no perceptual

differences are detected between forward and reversed aggressive calls, whereas reversed food and alarm calls sound distinctively different from forward exemplars.

Results revealed that rhesus switched from a right to a left ear orienting bias for both harmonic arches and shrill barks played backwards. However, for the aggressive calls, rhesus maintained a moderate right ear bias. These data are consistent with the description of each call's characteristic amplitude envelope. Reversing a relatively symmetric call has little to no effect on the orienting response, whereas reversing an asymmetric call directly influences the direction of the orienting bias. In parallel with the manipulations of inter-pulse interval (Hauser, et al., 1998), these results also suggest that the left hemisphere bias shown for normal, but not reversed calls, has to do with the specific, species-typical call morphology.

Patterns and problems

Results from all of the playback experiments described above are consistent with the interpretation that the left hemisphere is more active in processing conspecific vocalizations while the right hemisphere is more active in processing sounds falling outside the species-typical repertoire. One possible explanation of these patterns is that meaningful sounds (in terms of conspecific interactions) are preferentially processed in the left hemisphere while other acoustic signals (which may be meaningful in terms of particularly salient environmental events) are preferentially processed in the right hemisphere. Two observations provide some support for this hypothesis. The first comes from Hauser and Andersson's (1994) original study, and the use of the ruddy turnstone's alarm call as a control. It is quite possible that this call contains meaningful

information that may be used to predict the presence of humans, an event that may be particularly useful in predicting the delivery of monkey chow or attempts to trap rhesus for biomedical purposes. Before this hypothesis can be evaluated, additional experiments with other, potentially meaningful sounds must be conducted. For example, one could contrast the response given to turnstone alarm calls with the response given to human speech, as well as potentially meaningful, but non-biological sounds such as the arrival of the boat (which brings the researchers to the island) or the sound of the chow placed into the dispenser. The second piece of evidence comes from studies of baboons indicating a left ear/right hemisphere bias for processing musical chords, pure tones, and human consonants and vowels (Pohl 1983, 1984). In this case, it appears that the observed asymmetry is mediated by sounds that are unlikely to carry any meaning or significance to baboons. Additional experiments are needed in order to better determine to what extent the left hemisphere is specialized for processing conspecific signals.

Another issue that remains unresolved is the developmental course of the head turning bias. As mentioned above, Hauser and Andersson (1994) found that infants did not display a significant head turning bias. Future research should focus on tracking the developmental course of the head turning preference. If the left hemisphere bias develops as the infants learn the meanings of the vocalizations, then there may be corresponding behavioral changes in vocal production. Thus we may look for a relationship between acoustic experience and the head orienting bias. In addition, the relationship between hemispheric maturation and the head orienting bias also warrants further investigation.

To date, the manipulations used with this playback paradigm have focused on temporal features. Using sound synthesis techniques developed by Evan Balaban and Kim Beeman (Beeman, 1996), however, it is also possible to manipulate spectral parameters of rhesus calls by creating synthetic replicas; the technique exploits pitch contour algorithms as well as tools for extracting the amplitude envelopes of each harmonic. Hauser and Fitch (see Hauser, 1999) used a habituation-dishabituation paradigm to determine whether rhesus classify synthetic calls as functionally similar to natural exemplars. Briefly, the experiment involved habituating the subjects to a series of natural exemplars and then playing back a synthetic replica. If subjects failed to respond (i.e., do not orient toward the speaker) to the synthetic replica, then a post-test call from a different functional category was played to ensure that the failure to respond to the test signal was not due to the subject's overall habituation to the experimental setup. Preliminary results, using tonal screams and harmonic arches, revealed that rhesus transfer habituation to the synthetic exemplar, suggesting that the natural and synthetic exemplars are treated as functionally similar (see Hauser, 1999 for summary of experiment). These results are important only in so far as they set up a methodology for systematically manipulating the spectral properties of a call and then establishing which features most significantly contribute to the head turning bias.

Although behavioral studies of acoustic perception in macaques are relatively advanced with respect to our understanding of specialized processing, we do not know anything about the other species of primates. As we have emphasized throughout this chapter, comparative data are critical if we are to document the phylogenetic patterns

associated with cerebral asymmetries underlying acoustic perception. At present, we do not know whether macaques are typical or atypical in their perceptual biases.

If we focus on the macaques, and especially rhesus macaques, several issues remain. First, the head orienting method must be cross-validated with other species. Second, if rhesus preferentially turn the right ear to listen to conspecific vocalizations, what clockwise deviation from the center line (i.e., 180 degrees from the midpoint of the subject's back) is necessary to induce a shift from right to left ear for unmanipulated conspecific calls? This experiment would test the strength of the head orienting effect by testing it against directional cues. Third, for rhesus reared in captivity, with considerable exposure to human speech, is there a right ear/left hemisphere bias for both rhesus monkey calls and human speech? More specifically, is the orienting bias due to the frequency of exposure to rhesus calls or to an innately specified, specialized mechanism for processing conspecific calls? The fact that infants do not develop the species-typical orienting bias until after the first year of life is not evidence against an innate bias. Fourth, when do infants develop the species-typical orienting bias? Fifth, to what extent is the orienting bias flexible? If rhesus monkeys are cross-fostered (Masataka and Fujita, 1989, Owren et al., 1993) do they show the orienting bias of their own species, or of the cross-fostered parent? Sixth, what areas of the brain are most directly involved in the orienting bias? Data reviewed in section 5 provide some answers to this last question.

5. The neural bases of vocal perception

5.1 Gross anatomical differences between hemispheres

The perceptual asymmetries for vocal perception are supported by both neuroanatomical and experimental lesion studies, although here the data extend beyond the macaques. For humans that have demonstrated left-hemisphere biases for language processing, it has been shown that the Sylvian fissure (bordering auditory cortex) is significantly longer in the left hemisphere than in the right (Geschwind and Levitsky, 1968). It has been assumed that the length of the fissure corresponds to the size of auditory cortex. Based on this assumption, potential anatomical asymmetries have similarly been measured in several primate species. Left Sylvian fissure length was found to be significantly greater than right for apes (*Pan*, *Gorilla*, and *Pongo*; LeMay and Geschwind, 1975), Old World monkeys (*M. fascicularis* and *M. mulatta*), and New World monkeys (*Saguinus oedipus* and *C. jacchus*)(Falk *et al.*, 1986; Heilbronner and Holloway, 1988). These results support the claim that the perceptual asymmetries observed under laboratory (Petersen *et al.*, 1984) and semi-natural (Hauser and Andersson, 1994) conditions are associated with these anatomical asymmetries.

Recently, more detailed analyses of potential asymmetries in the primate auditory cortex have revealed specific homologies with the language areas in humans. For instance, an auditory cortical structure known in ape and human brains as the *planum temporale* is located in the posterior portion of the temporal lobe. In the majority of humans, this structure is significantly larger in the left hemisphere than the right and is considered a speech processing area (Geschwind and Levitsky, 1968). A similar left-

right asymmetry in the planum temporale has been shown for chimpanzees and other great apes (Gannon *et al.*, 1998a; Gannon *et al.*, 1998b). In an Old World monkey species (*Macaca fascicularis*), volumetric measurements of the cytoarchitectonic area Tpt, which is the equivalent of the planum temporale in humans and pongids, revealed that the left area Tpt was significantly larger than the right (Gannon *et al.*, 1999).

Interestingly, the left Tpt appeared to have a unique neurochemical organization when compared to the right Tpt (Kheck *et al.*, 1999). Specifically, the left Tpt had greater parvalbumin (a calcium-binding protein) and GABA (an inhibitory neurotransmitter) immunoreactivity, while the right Tpt had greater calbindin (another type of calcium-binding protein) immunoreactivity. These data suggest that the neurochemical specialization of the language areas evolved prior to the gross anatomical asymmetries (Kheck *et al.*, 1999).

5.2 Lesion studies of the auditory cortex

Human patients with lesions of the left temporal lobe exhibit deficits in speech perception (Mazzocchi and Vignolo, 1979), a phenomenon known as Wernicke's aphasia. This deficit is specifically associated with lesions in the posterior portion of the left temporal gyrus, an area that contains higher-order auditory areas, such as the planum temporale (area Tpt in Old World monkeys). In rhesus macaques and squirrel monkeys, experimental lesions of auditory cortex result in a similar deficit, in that subjects become selectively impaired at discriminating species-specific vocalizations but not other types of auditory stimuli (Dewson, 1977; Heffner and Heffner, 1984; Heffner and Heffner, 1986; Hupfer *et al.*, 1977). The performance of Japanese macaques trained to discriminate

between the two different coos used in the behavioral asymmetry studies (Petersen *et al.*, 1984, see section 4.2) was greatly impaired following lesions of the left superior temporal gyrus, but was unimpaired by similar lesions in the right hemisphere (Heffner and Heffner, 1984; Heffner and Heffner, 1986).

In squirrel monkeys, bilateral lesions of auditory cortex impaired performance of vocal discrimination (unilateral lesions did not), but this deficit was not specific to vocalizations (Hupfer *et al.*, 1977). The gross neuroanatomical data converge with the absence of neural lateralization in squirrel monkeys: Sylvian fissure asymmetries are not as robust in this species as in other primates (Heilbronner and Holloway, 1988). This leads to the conclusion that in squirrel monkeys, unlike Japanese macaques, auditory cortex processes vocal signals in the same way as it processes other complex sounds (Hupfer *et al.*, 1977).

Patterns and problems

A synthesis of current results suggests that the left auditory cortex of Japanese macaques is specialized for processing vocalizations, whereas squirrel monkeys appear to lack such specialization. These findings underscore the importance of choosing an appropriate species to answer particular neuroethological questions, and caution against making generalizations from one primate species to all primates (Preuss, 1995). This is particularly important given that most neurophysiological experiments using species-specific vocalizations have used squirrel monkeys (see below). It would be of significant interest to determine whether other species of primates, which show Sylvian fissure asymmetries, demonstrate behavioral asymmetries in the processing of their conspecific vocalizations. This would directly test whether neural asymmetries (or lack

thereof) mediate behavioral asymmetries, an important relationship given the findings for human speech.

Given the rather crude spatial resolution of these types of lesion experiments, it is unclear what specific auditory cortical areas are contributing to the behavioral asymmetries. In both the Japanese macaque and squirrel monkey studies, much or all of the superior temporal gyrus was removed. The temporal lobe contains many auditory and auditory-related cortical areas (Kaas and Hackett, 1998). Based on the anatomical studies conducted thus far, one would predict that area Tpt would be critically involved in macaques (Gannon *et al.*, 1999; Kheck *et al.*, 1999).

A second difficulty associated with lesions studies is that they are confounded by the problem of behavioral recovery. For example, although the ability of Japanese macaques to discriminate conspecific calls was impaired following lesions of the left auditory cortex (Heffner and Heffner, 1986), they regained normal performance after 5 to 15 sessions. Thus, there is considerable, and rapid, neural plasticity following experimental lesions that cannot be controlled. Similar issues arise in studies of lesions in human patients (Naeser *et al.*, 1987).

Again, many questions regarding neural asymmetries in primates may best be addressed by functional imaging techniques (Logothetis *et al.*, 1999). Such an approach would offer better resolution, at the level of cortical areas, while avoiding sampling errors associated with electrophysiological methods. In comparison with lesion experiments, functional imaging would avoid non-stationary effects such as lesion-induced plasticity and problems controlling the extent of lesions. An illustrative experiment would involve imaging the temporal lobe of a rhesus macaque while presenting normal versus temporally manipulated calls (ISI manipulations or reversed calls). Given this species' differential head orienting responses to these call categories,

this would allow us to determine differences in the hemispheric distribution of active cortical areas under both conditions.

5.3 Call-selective neurons in the auditory cortex

To date, the squirrel monkey represents the most extensively studied mammalian model system for the auditory processing of species-specific vocalizations. This is, in one sense, an unfortunate situation given the fact that most of the work was conducted before 1975; on the other hand, it speaks to the great insights of this team of researchers (reviewed in Jürgens 1990; Hauser 1996). Recordings of single unit activity in the superior temporal gyrus of the awake squirrel monkey revealed that more than 80-90% of the neurons in this region responded differentially to more than one of the 12 species-specific vocalizations used as stimuli (Newman and Wollberg, 1973; Wollberg and Newman, 1972). For one subpopulation of neurons, a variety of temporal firing patterns were observed across the sample of neurons for any given call type. Likewise, the firing pattern of a given neuron varied considerably as a function of call type. In another subpopulation, neurons responded selectively to one vocalization and had a relatively simple discharge pattern (Wollberg and Newman, 1972; Winter and Funkenstein, 1973). Although the relative lack of information regarding squirrel monkey architectonic boundaries in these studies limits what one can say about the functional organization of auditory cortex, they nevertheless provide substantial evidence that auditory neurons are highly responsive to species-specific vocalizations, and sometimes highly selective for vocalizations.

More recent experiments in identified subdivisions of auditory cortex of anesthetized rhesus and marmoset monkeys largely support the results from squirrel monkeys, demonstrating

that cortical neurons, from multiple subdivisions of the auditory cortex, selectively respond to conspecific vocalizations with complex temporal patterns of firing (Rauschecker *et al.*, 1995; Tramo *et al.*, 1996; Wang *et al.*, 1995). Rauschecker *et al.* (1995), using vocalizations recorded from rhesus monkeys as stimuli, found several call-selective neurons localized to area Tpt of the superior temporal gyrus—an area homologous with the planum temporale (Wernicke’s area) in humans.

Patterns and problems

Given that auditory cortical neurons can be call-selective, or at least call-responsive, how are these complex spectrotemporal stimuli integrated by such neurons? In other words, how is selectivity achieved? One approach to answering these questions involves presenting acoustically manipulated stimuli. One can systematically alter specific features of a call and then use such perturbed signals to determine how components of the call affect neural response patterns. As has been demonstrated in the songbird (Margoliash, 1983; Margoliash and Fortune, 1992) and bat auditory systems (Suga *et al.*, 1987; Kanwal 1999), this approach has revealed that neurons are sensitive to particular conjunctions of acoustic features as opposed to isolated components of the vocal signal. In rhesus macaques, filtering out certain frequencies (or selectively removing harmonics) in particular species-specific vocalizations (such as the ‘coo’ call), results in less robust responses from call-selective neurons when compared to responses to normal, intact vocalizations (Rauschecker, 1998; Rauschecker *et al.*, 1995). Similarly, in the temporal domain, it has been shown that editing out parts of, or reversing, vocalizations used as stimuli results in a decrease in neuronal responsiveness for call-

selective neurons in squirrel monkeys (Wollberg and Newman, 1972), marmosets (Wang *et al.*, 1995), and rhesus monkeys (Rauschecker, 1998). Together with studies of ‘response enhancement’ using tone sequences as stimuli (Brosch *et al.*, 1999), these data suggest that neurons in the auditory cortex of primates are ‘combination-sensitive’ (i.e. they respond nonlinearly) to conspecific vocalizations in the same way that neurons in the songbird forebrain and bat auditory cortex are combination sensitive to their own vocalizations.

Several questions remain concerning the behavioral relevance of the selectivity of primate auditory neurons. For example, how do spectrotemporal manipulations that affect responses at the *neural* level affect responses at the *perceptual* level, and vice versa. Does removing or extending particular portions of vocalizations affect how subjects respond to them? How are the temporal manipulations of vocalizations that influence behavior processed by call-selective neurons in the auditory cortex (Hauser *et al.*, 1998)? What is the relative importance of temporal versus spectral cues in vocal processing. Different domains may be used to extract different categories of information. For example, temporal features may define whether a call is within the conspecific repertoire (Hauser *et al.*, 1998), while spectral features may define the identity (or size) of the caller (Fitch, 1997; Rendall *et al.*, 1996). Finally, what is the distribution of call selective neurons in the right and left hemispheres, and do split-brain monkeys show cerebral dominance for processing species-typical vocalizations? Future studies must not only address these questions, but extend the range of species studied beyond squirrel monkeys and macaques.

6. Specialized processing of facial expressions and vocalizations: production mechanisms

6.1 Production of facial and vocal expressions: behavior and context

Humans produce a wide range of different facial expressions (Darwin, 1872; Ekman, 1973; Fridlund, 1994). While considerable variation exists between different populations, humans around the world are able to recognize at least six basic emotions (Ekman, 1992). Such universality may indicate that humans have an innate capacity for both expressing and perceiving facial expressions. Further evidence for this claim comes from studies of human infants. For example, infants spontaneously start producing smiles within the first few weeks of life, even though there is considerable cross-cultural variation in the frequency with which parents smile at their infants (Trevathen 1979). Moreover, blind infants start producing smiles at the same time as infants born with normal eyesight, suggesting that visual feedback is not necessary for the production of smiles (Eibl-Eibesfeldt, 1973). Finally, smiles have a consistent, stereotyped structure, and generally convey the same emotional state for humans throughout the world.

Darwin (1872) was perhaps the first to point out the continuity in the expressions of humans and nonhuman animals. Although he explicitly avoided providing an adaptationist's perspective, he nonetheless maintained that the observed similarity provided support for his theory of evolution by natural selection (Fridlund, 1994). Since his landmark book entitled The Expression of Emotions in Man and Animals, other researchers have proceeded to show quantitatively that Darwin's observations were indeed correct. Some of the most striking continuities in facial expressions occur between humans and primates. Preuschoft & van Hoof (1997) argue that the

morphological similarities between the "bared teeth" and "open mouth" displays of many primate species, and the smile and laughter expressions produced by humans, are homologous across all primate species. They suggest that these expressions evolved to mediate social interactions in primates. The phylogenetic continuities found in studies of human and primates suggest that some facial expressions are displays that evolved as a result of natural selection.

In contrast to the documented similarities between human and primate facial expressions, until recently, far less was known about homologs or analogs to human vocal expressions. Nonhuman animals, primates included, produce a range of different vocal expressions. As Darwin articulated, many of these sounds convey information about the caller's affective state (see also, Smith, 1977). Often, the connection between affective state and acoustic morphology is consistent across animals. For example, as Darwin, Morton (1977) and Hauser (1993) have revealed, vocalizations associated with aggression are often low pitched while vocalizations associated with fear or affiliation are often high pitched. Recent studies of primates, and one avian species (i.e., the domestic chicken), also provide evidence that some vocalizations convey information about events that are external to the caller (Seyfarth et al., 1980, Cheney & Seyfarth, 1982, Dittus, 1984, Gouzoules et al., 1984, Evans et al. 1994, Hauser, 1998, Zuberbuhler et al., 1997, 1999). While these calls are not equivalent to human words, they are not simply expressions of the caller's affective or internal state. Rather, such vocalizations appear to be functionally referential, with acoustic morphology closely coupled to key objects (e.g., predators, food) and events (e.g., dominance related social interactions) in the species-typical environment (Cheney & Seyfarth, 1990, Marler et al., 1992, Hauser, 1996).

Given the information conveyed, it is of interest to explore whether the patterns of hemispheric asymmetry exhibited for primate facial expressions are similar to or different from those exhibited for primate vocalizations.

6.2 Hemispheric asymmetries in the production of human facial and vocal expressions

Humans demonstrate asymmetrical use of the mouth during vocal and facial expressions. Specifically, one side of the mouth opens wider and is more expressive during the production of different facial and vocal expressions. Early work on facial expressions indicated that humans expressed emotions more strongly on the left side of the face than on the right side (Sackheim et al., 1978). In the past two decades, however, a different picture has emerged. While producing expressions associated with positive/approach emotions, humans exhibit a right side bias. In contrast, expressions mediated by negative/withdrawal emotions are associated with a left side bias (Davidson et al., 1990, Davidson, 1995). These data suggest that the different hemispheres are responsible for opposite aspects of emotional expression in humans. Whereas the left hemisphere is dominant for positive/approach expressions, the right hemisphere is dominant for negative/withdrawal expressions. Several studies using neuroimaging techniques on brain damaged and normal patients provide support for the relationship between emotional valence and hemispheric specialization during the production of expressions (Davidson, 1999).

Investigations of mouth asymmetries during speech production show a somewhat different pattern. Humans exhibit a strong lateral bias to the right side of the mouth while producing meaningful speech (Graves & Goodglass, 1982). This effect, however, is

somewhat variable depending on the task and the sex of the subject. Graves et al (1982) conducted four separate experiments to further explore asymmetrical use of the mouth during speech production. Male and female subjects were asked to either describe a scene or generate a list of words. While males showed a significant bias for the right side of the mouth for both of these tasks, female subjects showed the right side bias only for generating the word list. Only slightly more than half of the female subjects showed a right side bias while describing the scene (44 of 85). Since there have been no follow-up studies, we do not yet know whether certain types of words (i.e. vowel, nouns, adjectives, etc.) show greater asymmetries than others, or whether different speech acts (e.g., producing nonsense words with linguistically relevant intonation or rhythm) cause other patterns of asymmetries in mouth use. More research in this area is likely to elucidate our knowledge of the asymmetrical use of the mouth during speech production.

6.3 Hemispheric asymmetries in the production of primate facial and vocal expressions

Hauser (1993) conducted an analysis of adult rhesus monkey facial expressions to explore the possibility of hemispheric asymmetries. Video footage was taken of free-ranging rhesus monkeys producing four different facial expressions: the fear grimace, copulation grimace, open mouth threat and ear flap threat. Video records were then analyzed to determine which side of the face started the expression first, and which side was more expressive. For all facial expressions, rhesus monkeys showed a left side bias. To further explore this asymmetry, chimeras of the rhesus expressions were created for the right and left side of the face. Human subjects were then asked to rate the chimeras

for overall expressiveness. Forty-one of the forty-three subjects reported that the chimeras for the left side of the face were more expressive than the right side chimeras.

All of the expressions used in Hauser's analyses were associated with negative/withdrawal emotions, with the exception of the copulation grimace. Although the copulation grimace is produced by males during copulation, presumably an interaction associated with positive emotion, males are sometimes attacked during copulation (Hauser, 1993); the possibility of being attacked may cause the act of copulation to be associated with negative emotion as well. Overall, then, the pattern of results obtained suggest that, like humans, rhesus monkeys also exhibit right hemisphere dominance for facial expressions associated with negative/withdrawal emotions.

In a follow up study, Hauser (1999) found that in contrast to other facial expressions, adult and juvenile rhesus monkeys exhibited a right side bias while producing the play face. The play face is the only expression in the rhesus monkey repertoire that is clearly associated with positive/approach emotions. In contrast to adults and juveniles, Hauser found no evidence for a directional bias in the facial expressions of infants. The results of this study, together with Hauser's (1993) earlier report, suggest that the directional asymmetries exhibited by rhesus during the production of facial expressions are similar to those shown by humans. However, these studies were based on relatively small sample sizes, thus making the putative similarity with human facial expressions relatively tenuous.

To increase the sample of subjects, as well as the number of exemplars per facial expression type, Hauser & Akre (in press) conducted a follow-up study of rhesus monkey facial expressions. In addition to facial expressions, they also analyzed video records of

vocalizations and the gestures mediating their production. Their methodology followed that of Hauser (1993,1999), measuring the side of the mouth first initiating the expression. Results showed that adults exhibited a statistically significant left side bias during the production of four different vocalizations, but no side bias for four other vocalizations. The four facial expressions first measured by Hauser (1993) also showed a left side bias, but with a larger sample of subjects and exemplars per expression type. Given that the repertoire of facial expressions and vocalizations analyzed include signals associated with both positive/approach and negative/withdrawal emotions, these studies fail to support the hypothesis that the direction of asymmetry covaries with emotional valence. Thus, and in contrast to the earlier reports, adult rhesus monkeys show a significant right hemisphere/left side of the mouth bias for both vocal and facial expressions, given in a variety of emotional contexts. These results stand in contrast to the patterns obtained for humans, but support the general conclusion that rhesus monkeys show hemispheric asymmetries for producing communicative expressions.

Analyses of infants revealed a left side bias in three of the four vocalizations, and one of the three facial expressions. Because these expressions were associated with both positive/approach and negative/withdrawal emotions, the pattern exhibited by infants also provides no support for the emotional valence hypothesis. That is, infants show a right hemisphere bias for producing both facial and vocal expressions, independently of emotional content.

Insert Figure 2 Here

Hauser et al. (in prep) also analyzed the extent to which expressions remained lateralized over the course of the expression, as well as the degree to which the mouth opened wider on one side than on the other. In this study, asymmetries in mouth opening (i.e. area of the left and right sides) were scored from video for each frame for four different facial expressions and six different vocalizations (Figure 2). Specifically, for each frame the face was bisected by dividing the face into left and right sides with a line drawn directly down the midpoint of the face. The area was then determined by measuring the area of the open mouth on each side of the midpoint line. The data were analyzed for the following effects: the overall number of frames that showed a left versus right side bias in each expression, the side of the mouth initiating the expression and completing the expression, the magnitude of the asymmetry during an expression and, the within subject stability for producing a specific expression. Results indicated that adults show a left side bias for most vocal and facial expressions in the first three analyses. Additionally, the within-subject analyses indicated that subjects consistently showed the same lateral bias across exemplars. Infants, in contrast, showed moderately less asymmetry, but all expressions exhibiting statistically significant side biases were in the same direction as for adults: left side.

In parallel with the findings from Hauser & Akre (in press), the asymmetries revealed from the analyses of mouth opening can not be accounted for by the emotional valence hypothesis. Specifically, although those expressions showing statistically significant side biases were all biased to the left side, some of these expressions were associated with positive/approach emotions, and some with negative/withdrawal emotions. Taken together, studies of rhesus monkeys (Hauser, 1993, 1999; Hauser &

Akre, in press, Hauser et al., in prep) indicate right hemisphere dominance during the production of both facial and vocal expressions, independent of emotional content.

Asymmetrical use of the mouth during vocal production has also been shown in the common marmoset (*Callithrix jacchus*), a New World primate. Hook-Costigan & Rogers (1998) studied asymmetries in the production of the tsik and twitter vocalizations. The tsik call/expression is apparently associated with fear and is generally given when individuals come into contact with a predator. The expression can occur with the vocalization, but it is also given in isolation. The twitter is used as a social contact call (Epple, 1968). Based on contextual observations Hook-Costigan & Rogers argue that the tsik call/expression is associated with negative/withdrawal emotions, while the twitter is associated with positive/approach emotion. After recording video footage of captive adult marmosets producing these facial and vocal expressions, a frame-by-frame analysis was conducted to assess asymmetrical use of the mouth, as well as the stability of the lateral bias over the duration of the expression. Results indicated a left side bias during production of the tsik expression, with or without the vocalization, and a right side bias when the subjects produced twitter vocalizations. In addition, these side biases were maintained over the course of the entire expression. These results stand in contrast to the patterns obtained for rhesus monkeys, but converge with the directional asymmetries documented for humans.

6.4 Patterns and problems

The patterns of lateralization in marmosets appear to resemble those found in humans, while the patterns observed in rhesus monkeys expressions are different, the

latter showing exclusive lateralization to the left side of the mouth, for all expressions, both vocal and facial. There are several potential reasons for this difference. Hook-Costigan & Rogers only examined asymmetries associated with two vocalizations and one facial expression unaccompanied by any vocalisation, whereas Hauser and colleagues looked at four facial expressions and six vocalizations. At this point, we can not yet ascertain the extent to which the tsik and twitter expressions are representative of the entire repertoire of marmosets. As was the case with rhesus monkeys, some of the effects found with a small sample of expressions and individuals changed with a larger data set (Hauser & Akre, in press, Hauser et al., in prep). Therefore it is possible that with a larger sample of facial and vocal expressions, the lateralities reported in marmosets would show a different pattern, especially with respect to the association between emotional valence and hemispheric asymmetry. However, an alternative possibility is that the evolutionary pressures that led to lateralized facial and vocal expressions in these species caused different patterns of lateralization to develop. This possibility is supported by the fact that significant results were obtained for both marmosets and rhesus. Such species differences are not uncommon in studies of behavioral lateralization in primates (Bradshaw & Rogers 1994, McGrew & Marchant 1997). However, until more data are available for comparison, any of these possibilities may prove correct.

Researchers studying cerebral asymmetries in humans have differentiated between facial and vocal expressions. Typically, the lateralization associated with speech production is separated from expressions in which the face and mouth change but no sounds are uttered. Hook-Costigan & Rogers (1998) do not, however, make this

distinction. In their analysis, they apply the emotional valence hypothesis (Davidson, 1995) to both facial and vocal expression. Little is known about the relationship between affective changes and asymmetries in the use of the mouth during speech production. Therefore it would be premature to assume that all expressions, facial and vocal, will be lateralized according to the pattern found for facial expression. Clearly, more work is needed on human and primate expressions to fully understand the relationship between asymmetries at the level of the central nervous system and asymmetries at the periphery. Furthermore, we need to extend the comparative data beyond rhesus monkeys and marmosets, and provide more careful analyses of the underlying emotions as well as the communicative content of both vocal and facial expressions.

7. Neural mechanisms underlying the production of facial and vocal expressions

7.1 Neural control of orofacial movements

Surprisingly little work has been done on the neurobiology underlying the production of primate facial expressions. To our knowledge, the only study conducted to examine the contributions of the neocortex in the production of species-typical facial expressions is that of Ifune, Vermeire, and Hamilton (1984). Using split-brained rhesus macaques, these investigators compared the frequency with which visual stimuli such as natural scenes (including videos of humans and primates) could elicit facial expressions. They found that visual stimulation of the right hemisphere elicited significantly more facial expressions from their subjects than the left hemisphere.

At a more basic level, electrical stimulation of motor cortical areas has been used to delineate the representations of orofacial movements. In both the owl monkey (*Aotus*

trivirgatus) (Preuss *et al.*, 1996) and the genus *Macaca* (Gentilucci *et al.*, 1988; Goldshalk *et al.*, 1985; Huang *et al.*, 1988), it was found that electrical stimulation of the ventral regions of the primary motor cortex and the ventral premotor cortex can elicit facial and oral movements. However, the relationship between the movements evoked in these studies and species-typical expressions is ambiguous. Thus, although, these cortical areas could be involved in facial expressions, vocal production, and/or food consumption, they do provide a foundation for future studies of the motor control of facial expressions.

7.2 Cortical control of vocal behavior

In humans, electrical stimulation and lesion studies have demonstrated that motor, premotor, and prefrontal regions of the antero-lateral neocortex are involved in the specialized functions of speech (eg. naming, syntax, verbal memory, etc.) (Ojemann, 1983). In the majority of right-handed subjects, these functions are lateralized to the left hemisphere. The medial part of the anterior cerebral cortex—the mesial cortex—is also involved in human speech (Sutton and Jurgens, 1988). This region includes the anterior cingulate and supplementary motor area. Based on electrical stimulation and lesions studies, the mesial cortex appears to be involved in the less cognitive aspects of speech production such as the regulation of speech and the basic motor control of vocalizations (e.g. the initiation of a vocal response) (Sutton and Jurgens, 1988).

7.2.1. The cingulate and supplementary motor cortex

Using electrical stimulation and experimental lesions, at least some of the cortical regions involved in primate vocal production have been identified. Most of this work focuses on squirrel monkeys and macaques. In a series of intense studies using electrical

stimulation, Jürgens and his colleagues have mapped all the cortical and subcortical areas of the squirrel monkey brain which are involved in producing vocalizations (see Jurgens, (1992) for review). They found that the region around the anterior cingulate sulcus, which includes the supplementary motor area and limbic cortex, is the cortical region from which vocalizations can be elicited via electrical stimulation (Sutton and Jurgens, 1988). In support of these data, bilateral lesions of these areas reduce the number of spontaneous vocalizations, although different call types are affected differentially (Kirzinger and Jurgens, 1982).

Data from macaques are nearly identical to the results found for squirrel monkeys. Electrical stimulation of the anterior cingulate cortex and the supplementary motor area elicit vocalizations, although not nearly as many call types as in squirrel monkeys (Robinson, 1967; Sloan and Kaada, 1953; Smith, 1945). Lesions of these areas, as in the squirrel monkey, reduce the rate of vocalizations (Aitken, 1981; Sutton *et al.*, 1974; Sutton *et al.*, 1985). Furthermore, single unit studies have demonstrated vocalization-related neural activity in the mesial cortex of macaques (West and Larson, 1995). These results from squirrel monkeys and macaques suggest homologies with the vocalization-related areas of the mesial cortex in humans.

7.2.2. *The lateral motor cortical areas*

Studies of lateral neocortex have not established a clear-cut role for this region in primate vocal production. Electrical stimulation of the motor cortex in both squirrel monkeys and macaques elicits vocal fold movements (Hast *et al.*, 1974; Hast and Milojevic, 1966), but few, if any, vocalizations were elicited (Green and Walker, 1938).

Bilateral lesions of motor and premotor ‘face’ areas, presumptive homologues of Broca’s area in humans, do not appear to alter the acoustic structure of calls or the rate of calling in squirrel monkeys (Kirzinger and Jurgens, 1982) and macaques (Aitken, 1981; Sutton *et al.*, 1974). Thus, while the lateral precentral cortex may be involved in oral and laryngeal movements, its role in vocal behavior does not appear to be critical, based on current evidence.

7.3 Patterns and problems

The search for the evolutionary substrates underlying these vocalization-related areas has been only partially successful. To date, only squirrel monkeys and macaques have been studied extensively. Data from these species suggest that, like humans, the anterior cingulate cortex and supplementary motor area play an important role in vocal production. However, there is scant evidence for the participation of lateral neocortical motor areas in primate vocal behavior, and hemispheric asymmetries at the neural level have not been investigated.

In humans, higher order vocal control of speech is generally associated with areas in the lateral neocortex. It is unclear what role, if any, the lateral neocortical motor areas play in primate vocal production (Deacon, 1997), but the manner in which their potential role has been tested has not been thorough. For example, in human studies, it is known that the application of electrical stimulation to the lateral neocortex outside of the primary motor area of awake, but quiet human subject *does not* elicit speech sounds (Ojemann, 1983). It is only when stimulation is applied during an on-going language task that effects of stimulation can be identified. Thus, in the case of the primate studies, a more

fruitful approach may be to apply electrical stimulation during vocalizations, especially in primates that produce long, multi-syllabic calls (eg. cotton-top tamarins, capuchins, marmosets).

Another approach may be to use behavioral/lesion techniques in which the control of vocal production can be assessed by the experimental manipulation of external noise, followed by measuring the compensatory mechanisms used to transmit vocal signals. For example, voice amplitude in particular frequency bandwidths can be controlled by macaques in the presence of acoustic noise (Sinnott *et al.*, 1975). In conjunction with experimental lesions, such studies may reveal the neural basis for such exquisite motor control. Indeed, there is evidence that voice amplitude may be affected by lesions of the motor cortical ‘face’ area (Green and Walker, 1938).

A major limitation of many of these neural studies is that our knowledge of the acoustic structure and variation of primate vocalizations was quite limited at the time these studies were conducted. The technology was not available to carefully quantify potential changes in the acoustic structure of vocalizations following lesions. We now have behavioral and acoustic evidence in Old World monkeys that the spectral properties of their vocalizations are in part the result of articulatory gestures, such as the movement of the lips, tongue, and jaws (Hauser *et al.*, 1993; Hauser and Schön Ybarra, 1994). For example, quantitative examination of the ‘coo’ vocalization (used in all the macaque studies cited above) indicates that the changes in the position of the jaw are reliably associated with changes in the dominant frequency (i.e., resonance frequency), but not the fundamental frequency (Hauser *et al.*, 1993). Given that there are motor and premotor areas involved in voluntary oral movements in primates, including movements

of the jaw, it is natural to assume that they would play an important role in the articulatory control of vocalizations. However, this remains to be tested neurophysiologically.

8. Conclusions

In this chapter, we have attempted to provide a summary and synthesis of current studies aimed at specialized processing of facial and vocal expressions in primates. What emerges is that primates show evidence of behavioral, neurophysiological, and neuroanatomical asymmetries for the perception and production of facial and vocal expressions. What we can not yet account for is the pattern of variation across species, and in some cases, within species but across expression types. Some of this variation is likely to be explained by differences in experimental procedure. To better understand the evolution of hemispheric specialization for communicative expressions, future studies must sample a broader range of species, using comparable methodological procedures.

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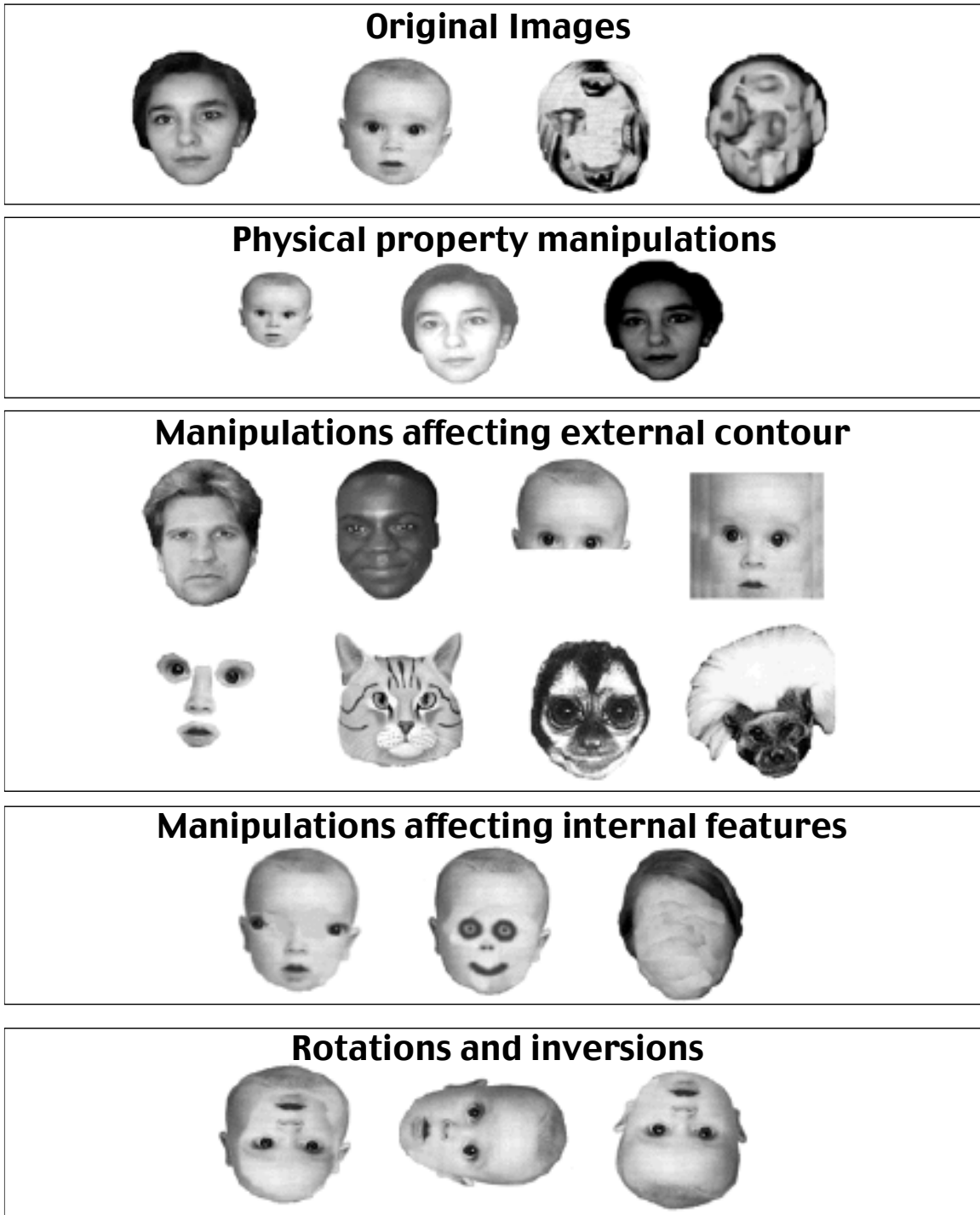


Figure 1 – Sample images from Weiss and Kralik (in press). The top row contains the original images that the tamarins were trained to discriminate. The remaining images are samples from the different categories tested during the experiment.

Copulation scream

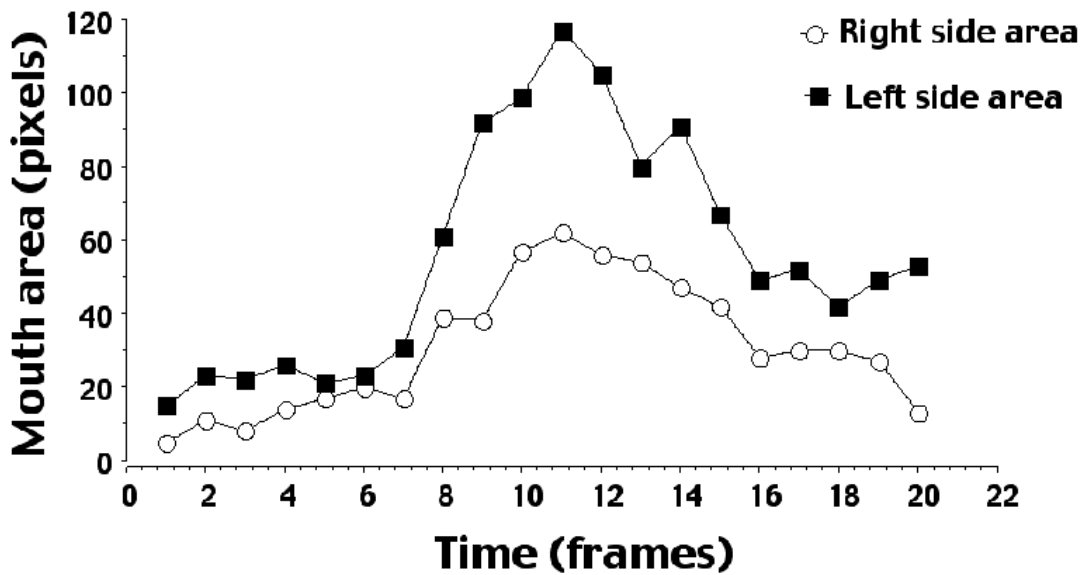
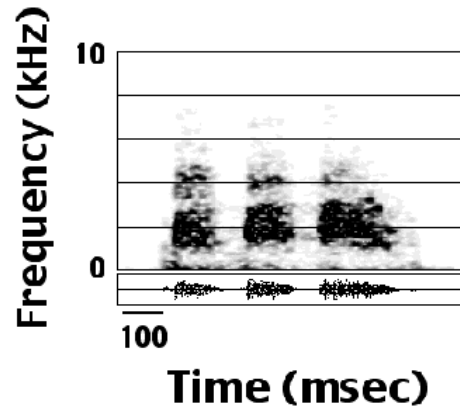
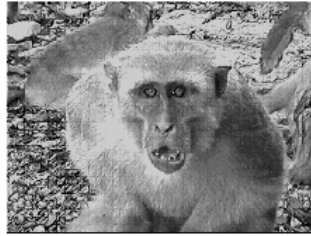


Figure 2 – Rhesus monkey producing a copulation scream. Second row: A spectrogram and smaller amplitude waveform of a copulation scream. Third row: A graph of the area asymmetry during production of a copulation scream.