



Asymmetries in the timing of facial and vocal expressions by rhesus monkeys: implications for hemispheric specialization

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Research on fish, amphibians, birds and mammals now provides considerable evidence of both anatomical and motor asymmetries. Most of this work focuses on motor actions related to handling objects or moving towards or away from them. Considerably less work has been conducted on motor actions associated with social interactions such as facial and vocal expressions. In this paper we present analyses of timing asymmetries for rhesus monkey, *Macaca mulatta*, facial and vocal expressions. We collected video records of semifree-ranging adult and infant rhesus monkeys during a variety of social interactions, and subsequently subjected them to frame-by-frame analyses. Results of these analyses revealed that both facial and vocal expressions are consistently produced by adults and infants with a timing asymmetry, with one side opening earlier than the other. Specifically, for both adults and infants, the left side of the face initiates the expression before the right, thereby implicating right hemisphere dominance. Because some expressions are related to positive/approach emotions while others are associated with negative/withdrawal emotion, emotional valence does not appear to influence the direction of this motor asymmetry. Results are discussed in light of potential differences between the mechanisms underlying the production and perception of communicative expressions in human and nonhuman primates.

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Over the past 10 or more years, studies of fish, amphibians, birds and mammals have revealed evidence of asymmetries in motor output (Bradshaw & Rogers 1993; Ward & Hopkins 1993; Davidson & Hugdahl 1995; Bisazza et al. 1998; Suthers 1999). Most of these studies have explored motor actions, such as which hand or foot is most involved in manipulating an object, or which side of the body turns to orient to a sound, smell or visual stimulus (Hopkins & Bennett 1994; Cantalupo et al. 1995, 1996; Hopkins & Bard 1995; Vallortigara et al. 1998, 1999). Relatively fewer observations have been collected on motor actions that are relevant to social interactions. Exceptions to this pattern are studies of avian song production and perceptual orientation (Nottebohm & Nottebohm 1976; Goller & Suthers 1995; Floody & Arnold 1997; Suthers 1999), as well as a few studies of primate face and vocal perception (Petersen et al. 1978; Heffner & Heffner 1984; Hamilton & Vermeire 1988, 1991; Hauser 1993b, 1999; Hauser & Andersson 1994;

Hauser et al. 1998; Hook-Castigan & Rogers 1998; Perrett et al. 1988; Vermeire & Hamilton 1998). In this paper, we present results from an analysis of rhesus monkey facial and vocal expression that provide evidence for motor asymmetries, and thus, presumed hemispheric specialization. This study therefore builds on our earlier work, in addition to ongoing studies of the mechanisms of vocal production in rhesus monkeys (Hauser 1992; Hauser et al. 1993; Hauser & Schön Ybarra 1994; Fitch & Hauser 1995; Fitch 1997).

Studies of human facial expression and speech articulation tend to reveal the following patterns. For facial expressions associated with negative/withdrawal emotion (e.g. fear, disgust), the left side of the face begins moving into the expression earlier than the right, and is more expressive. In contrast, for facial expressions associated with positive/approach emotion (e.g. happiness), the right side of the face starts earlier than the left and is again more expressive than the left side (Gainotti 1972; Sackeim et al. 1978; Sackeim 1982; Gazzaniga & Smiley 1991; Borod 1993; Davidson 1995). Although not all studies of human facial expression find such patterns (e.g. Blair et al. 1999), the right hemisphere generally plays a more dominant role in negative/withdrawal emotion, while the left hemisphere plays a more dominant role

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in positive/approach emotion (for recent reviews, see Davidson 1995, 1999; Adolphs 1999).

Relative to our understanding of facial expression, we know much less about asymmetries underlying speech articulation. Most of the research comes from the laboratory of Graves and colleagues (Graves et al. 1982, 1990; Graves & Landis 1985, 1990; Graves & Potter 1988) where observations and experiments indicate that the right side of the mouth opens before the left during speech production. In Broca's aphasics with damage to the left hemisphere, a right side of the mouth bias is observed for spontaneous speech, repetition and word list generation, whereas a left side of the mouth bias is observed for serial speech (counting to 10) and singing (familiar rhymes; Graves & Landis 1985). This difference suggests that when an automatic motor sequence is enlisted for vocal production, the right hemisphere is dominant. In contrast, even Broca's aphasics show left hemisphere dominance for nonautomatic vocal articulations, specifically those involving speech articulation.

The facial and vocal expressions of nonhuman primates clearly convey information about the signaller's emotional state (reviewed in Darwin 1872; Morton 1977; Hauser 1993c; Preuschoft 1995), and some have argued that they also convey information about objects and events in the external environment (reviewed in Cheney & Seyfarth 1990; Marler et al. 1992; Hauser 1996). In a study of asymmetries in primate facial expression, results from a relatively small sample of adults showed a consistent left side of the face bias, implicating right hemisphere dominance (Hauser 1993b). Specifically, the left side of the face started before the right side and was also more expressive. Since all of the facial expressions explored in this study were associated with negative/withdrawal emotions, it was not possible to test for differences in hemispheric specialization as a function of emotional valence (Davidson 1995). Unfortunately, there is only one facial expression within the rhesus monkey's repertoire that is unambiguously associated with positive/approach emotion: the 'play face' used primarily by juveniles, yearlings and infants during play. Copulation screams (Hauser 1993a), although seemingly associated with positive emotions linked to mating, are often met with aggressive attacks by other males, and thus, are potentially coupled with a negative emotion (see Results, Table 1). In a pilot study, Hauser (1999) found suggestive evidence that during the production of a play face, the right side of the face begins moving before the left. This result, however, was based on a small sample size, thereby leaving the emotional valence hypothesis untested. The results of the pilot study also suggested that juveniles and infants may show more variability in their expressions and less consistency in the direction of facial asymmetry than adults. This hypothesis also requires further testing with a larger sample of subjects and expressions.

In contrast to the work on facial expression, much less work has been carried out with respect to asymmetries in vocal expression even though knowledge of the mechanisms guiding vocal articulation are relatively advanced (Owren & Bernacki 1988; Hauser 1992; Hauser et al. 1993; Hauser & Schön Ybarra 1994; Fitch & Hauser 1995; Fitch

1997; Rendall et al. 1998). In a recent study of common marmosets, *Callitrix jacchus*, however, Hook-Castigan & Rogers (1998) found that the left side of the mouth opened more during the production of a fear expression or a mobbing call, while the right side of the mouth opened more during the production of a contact call. Based on behavioural observations, the fear expression and mobbing call appear to be associated with negative/withdrawal emotion, while the contact call is associated with positive/approach emotion. Given these patterns, the marmoset data provide support for the emotional valence hypothesis. What is not yet known is whether this pattern generalizes to other calls or expressions in the marmoset repertoire, and to both adults and infants.

A contrast between facial and vocal expressions is of considerable interest given the available data on humans, and recent work on vocal production and perception in rhesus monkeys. Specifically, if some macaque vocalizations are 'language-like', perhaps conveying functionally referential information as some have suggested (Gouzoules et al. 1984; Hauser & Marler 1993; Fischer 1998; Hauser 1998), then like speech articulation, rhesus should show a right side of the face/left hemisphere bias during production of functionally referential calls. In contrast, if rhesus vocalizations primarily convey information about affective state, then like facial expressions, they too should show a left side of the face/right hemisphere bias. Preliminary data also suggested that for some vocalizations, no timing asymmetries exist, whereas for other vocalizations, the right side of the mouth opens before the left side. One interesting contrast was between the 'fear grimace' and the 'scream'. These two expressions are produced with virtually identical kinematics, both involving retraction of the lips and a separation between the teeth (see Table 1). While the fear grimace is produced with a left side of the face timing bias, the scream appears to be produced with a right side of the face bias. This pattern requires more careful investigation with a larger sample of subjects and vocalizations.

Complementing the work on vocal production, studies of rhesus monkeys and Japanese macaques, *M. fuscata*, suggest that the left hemisphere is dominant during call perception. In particular, operant studies of Japanese macaques and rhesus monkeys reveal a right ear advantage for both accuracy and reaction time during discrimination of conspecific calls (Petersen et al. 1978; C. LePrell, M. D. Hauser & D. Moody, unpublished data). Field studies of adult rhesus monkeys reveal a right ear bias for orienting to conspecific calls, but a left ear bias for orienting to heterospecific signals (Hauser & Andersson 1994; Hauser et al. 1998b); infants under the age of 1 year failed to show an orienting bias. Hauser et al. have suggested that the orienting bias may be due to a left hemisphere bias for processing conspecific vocalizations. Lastly, studies on Japanese macaques (Heffner & Heffner 1984) reveal that performance on an auditory discrimination task involving two conspecific vocalizations deteriorates following lesions of the left auditory cortex, but not of the right auditory cortex. If the neural system underlying perception of vocalizations is lateralized to the same side of the brain as the system underlying

production of vocalizations, as appears to be the case for human language, then rhesus monkeys would be expected to show a left hemisphere/right side of the face bias during the production of vocal expressions.

The goal of this paper is to address three problems concerning asymmetries in the timing of facial and vocal expressions. First, is the timing of rhesus monkey facial and vocal expressions largely asymmetrical or symmetrical, and is the pattern expressed in adults similar to or different from younger animals? Second, if facial and/or vocal expressions exhibit timing asymmetries, are expressions associated with negative/withdrawal emotion produced with a left side of the face bias, whereas expressions associated with positive/approach emotion produced with a right side of the face bias? Third, if timing asymmetries are observed, are there differences between facial and vocal expressions, as appears to be the case in humans?

METHODS

Subjects

Observations of rhesus monkeys living on the island of Cayo Santiago, Puerto Rico were collected from May 1995 to August 1999. During this period, population size fluctuated from approximately 900–1300 individuals, while the number of social groups varied from seven to nine. Subjects are well habituated to the presence of human observers, and all individuals older than 2 years have leg and chest tattoos, as well as ear notches. In general, individuals have access to the entire island, and in this sense are considered semifree-ranging. Due to the hierarchy among groups, however, the highest-ranking groups often control access to certain parts of the island.

There are no predators on the island. Subjects are provisioned with monkey chow once each day. In addition to monkey chow, the diet consists of naturally available fruits, flowers, leaves, grasses and soil. Further information about this population and its history can be found in [Rawlins & Kessler \(1987\)](#).

Sampling Procedure

Due to the difficulty of obtaining high-quality video footage of animals vocalizing or producing facial expressions, we adopted an opportunistic sampling procedure. Each day, during 0700–1500 hours, a team of researchers would walk around the island, looking for animals engaged in social interactions. Either before an interaction started, or sometime thereafter, filming would begin. In each case, the researcher attempted to place him or herself in such a way that the target animal's face was centred in the viewing field, and flush with the camera. Because we were interested in scoring facial asymmetries, we attempted to minimize any tilt in the animal's head with respect to the camera angle ([Hauser 1993b, 1999](#)).

We sampled individuals from all age–sex classes and obtained data from 42 adult males, 77 adult females,

26 Juveniles and 55 infants. Juveniles were defined as individuals between the ages of 1 and 3 years, whereas infants were individuals 1 year old and younger. Females reach reproductive maturity at around 3 years of age, whereas males reach reproductive maturity at approximately 4 years.

We obtained video footage using a JVC-DV1 digital camera. We transferred the field footage onto a Macintosh computer using either an Apple or Radius video board and the Adobe Premiere video software. This system allowed us to step through a facial or vocal expression frame by frame; sampling rate was 30 frames/s. Each video record was stored as a separate file. To prevent biases in scoring, we flipped half of the files in the horizontal plane. Consequently, when observers scored each file for temporal asymmetries in the expression, they were unaware of the actual orientation of the subject with respect to the camera. Once a file was scored, we referred to a master list to determine whether it had been flipped from the original.

As in previous analyses ([Hauser 1993b, 1999](#)), we scored each expression for timing asymmetry or symmetry. An expression was scored as asymmetrical if, on the first frame in which the mouth opened, one side opened before the other; such asymmetries occur if the lips open on one side before the other, or if the jaw drops on one side before the other. An expression was scored as symmetrical if, on the first frame in which the mouth opened, both sides opened simultaneously. These analyses represent a first step in our attempt to characterize motor asymmetries during facial and vocal expression; analyses currently underway (M. D. Hauser, K. Akre & D. Goldenberg, unpublished data) explore asymmetries in timing at other temporal points in the expression, as well as differences in overall mouth opening (i.e. area).

A total of 40 film clips were scored by three different observers. Using [Cohen's \(1960\)](#) kappa to assess agreement between observers, we obtained scores of 0.67 and 0.77; these values fall within the 'good' to 'excellent' range based on the analyses of [Fleiss \(1981\)](#).

The Rhesus Monkey's Facial and Vocal Expression Repertoire

Rhesus monkeys produce a variety of facial and vocal expressions, and previous work has attempted to characterize this repertoire ([Rowell & Hinde 1962](#); [Gouzoules et al. 1984](#); [Hauser 1993a, 1999](#); [Hauser & Marler 1993](#); [Hauser & Schön Ybarra 1994](#); [Hauser et al. 1993](#); [Rendall et al. 1996](#)). Given the difficulty of acquiring high-quality video, the repertoire analysed in this report represents only a subset of the overall repertoire.

[Table 1](#) presents a list of the rhesus facial and vocal expressions we analysed together with a general description of the relevant contextual and kinematic details. We also provide a coarse-grained classification of each expression in terms of the negative/withdrawal to positive/approach continuum. There are at least two problems with this classification scheme. First, some negative

Table 1. Description of rhesus monkey facial and vocal expressions

Expression	Context	Kinematics
Facial		
Copulation grimace* Positive-approach	Given by adult males during copulation	Lips are retracted and teeth are clenched
Fear grimace† Negative-withdraw	Given by subordinates to dominants	Lips are retracted, showing the teeth (unclenched)
Lip smack‡ Negative-approach	Given by subordinates to dominants; sometimes also given by individuals grooming each other	Lips are smacked together rapidly, often resulting in a clicking noise
Open-mouth threat§ Negative-approach	Given by dominants to subordinates	Mouth is opened and placed into an O-configuration, with slight lip protrusion
Play face Positive-approach	Given by infants, yearlings and juveniles while playing	Mouth is opened wide and placed into an O-configuration, similar to the open-mouth threat; lips cover up teeth
Vocal		
Bark‡§ Negative-approach	A high-level aggressive call given by a dominant to a subordinate	Mouth is opened either wide as in the open-mouth threat or slightly less; lips are occasionally protruded forward
Coo Positive-approach	A contact call given during affiliative interactions such as grooming, eating and approaching	Mouth can be either opened wide or not at all; when opened, lips are often protruded forward
Copulation scream* Positive-approach	A call given by males during copulation	Lips are retracted and teeth are clenched
Grunt Positive-approach	A call given during affiliative interactions such as grooming and eating	Slight mouth opening and lip protrusion
Gecker Negative-approach	A call given by distressed infants, usually following maternal rejection	Mouth open slightly, with rapid lip opening and closing cycle
Girney‡ Positive-approach	A call given by an individual initiating a social interaction such as grooming or infant handling	Given with the mouth almost completely closed; lips move around in a chewing motion
Harmonic arch Positive-approach	A call given by an animal that has discovered a high-quality, rare food item	Starts with relatively closed mouth, and then opens wide in rounded configuration
Pant threat Negative-approach	A low-level aggressive call given by a dominant to a subordinate	Slight mouth opening and lip protrusion
Scream† Negative-withdraw	A call given by a subordinate being attacked by a dominant	Lips are retracted, revealing unclenched teeth

*†‡§§Symbols refer to facial expressions and vocal articulations that have the same or similar kinematics. For example, the fear grimace and scream share the same kinematics, a retraction of the lips (†).

emotions are associated with withdrawal while others are associated with approach. Thus, for example, open-mouth threats, barks and pant threats are each associated with a negative emotion (aggression), but the signaller approaches rather than withdraws from the receiver. Rather than force an expression into the existing dichotomy, we have attempted to use the negative–positive emotional continuum as one dimension, and the withdrawal–approach as a second dimension. Second, some expressions are associated with relatively more ambiguous emotional states. As mentioned earlier, for example, copulation screams would appear to be associated with the positive emotion of copulation. However,

because competition for mates is often high, a copulating pair will sometimes be attacked by other males lacking a mate; the threat of attack could make the emotion associated with copulation somewhat negative. Similarly, although lip smacks appear to be associated with a negative emotion given that they are produced by subordinates approaching dominants, they are also produced by individuals involved in grooming; the latter would appear to be associated with positive emotions. Given this ambiguity, the classification scheme presented in Table 1 should be seen as a working model of emotional valences in expression, one that will require much more careful analysis.

Table 2. Tests of whether facial expressions are significantly more asymmetrical than symmetrical

Expression	Age	Number of individuals	Number of expressions		Sign test <i>P</i>	Mean asymmetry index	<i>t</i> (<i>df</i>)	<i>P</i>
			Asymmetric	Symmetric				
All expressions	Adult	54	169	8	0.0001	0.84	8.39 (17)	0.0001
Copulation grimace	Adult	7	13	0	0.0002	1.0*	(1)	—
Fear grimace	Adult	16	25	0	0.0001	1.0*	(3)	—
Lip smack	Adult	15	72	4	0.0001	0.83	7.53 (8)	0.0001
Open-mouth threat	Adult	26	59	4	0.0001	0.76*	(3)	—
All expressions	Infant	18	77	3	0.0001	0.97	5	0.0001
Fear grimace	Infant	9	13	0	0.0002	1.0*	(1)	—
Lip smack	Infant	5	23	0	0.0001	1.0*	(1)	—
Play face	Infant	5	16	2	0.001	0.90*	(1)	—
Open-mouth threat	Infant	6	25	1	0.0001	—	—	—

*Sample too small for statistical testing.

Statistics

To determine whether facial and vocal expressions are produced asymmetrically, we first analysed each expression type with respect to the number of asymmetric versus symmetric exemplars. We restricted our analyses to expression types with a minimum of five individuals. To alleviate problems associated with variance in sample size among individuals, within expression types, no more than 10 exemplars per individual per expression type were used; for subjects with more than 10 exemplars, we used a random number generator to reduce the data set to 10. Furthermore, we analysed each expression type by subdividing the overall sample into adults, juveniles and infants. We then used a sign test to determine, within each expression type, whether a majority of exemplars were symmetrical or asymmetrical. To determine whether asymmetrical expressions were significantly biased to the left or right, we coded each exemplar with a left bias as 'L' and each exemplar with a right bias as 'R'. We then used sign tests to determine whether rhesus exhibit a significant left or right side bias for expression type. All sign tests were two-tailed, with significance set at $P < 0.05$.

We also conducted analyses at the individual level. To obtain a single value, we calculated an asymmetry index for each individual within each expression type by subtracting the number of symmetric exemplars from the number of asymmetric exemplars and dividing by the total number of exemplars. Positive values are thus associated with asymmetric timing, whereas negative values are associated with symmetric timing. We also used this index to determine the direction of timing asymmetries by subtracting the number of right-biased exemplars from the number of left-biased exemplars, and then dividing this value by the total number of exemplars. Positive values are thus associated with left side biases, whereas negative values are associated with right side biases. These indices were then entered into a one-sample *t* test with a hypothesized mean of 0.0; tests were two-tailed with significance set at $P < 0.05$.

RESULTS

Are Rhesus Facial Expressions Asymmetric or Symmetric?

Analyses of four facial expressions produced by adult rhesus monkeys revealed strong evidence of a timing asymmetry (Table 2). Of 177 facial expression exemplars, 169 showed a side bias ($P < 0.0001$). More specifically, when producing copulation grimaces, fear grimaces, lip smacks and open-mouth threats, adults initiated these expressions with either the left or right side leading.

At the individual level, the asymmetry index revealed evidence of asymmetries for all expression types, although due to sample size constraints, *t* tests could only be calculated for lip smacks.

Although preliminary analyses of timing asymmetries (Hauser 1999) suggested that infants were more variable than adults, results presented in Table 2 show that infants consistently produce facial expressions with a right or left side timing bias. Of 80 exemplars, 77 showed a side bias ($P < 0.0001$). More specifically, one side of the infant's mouth tended to open before the other for fear grimaces, lip smacks, play faces and open-mouth threats. At the individual level, calculations of the asymmetry index also revealed asymmetries, but due to the small number of individuals producing a sufficient number of exemplars, we were unable to carry out *t* tests on the data.

Are Rhesus Vocal Expressions Asymmetric or Symmetric?

Analyses of eight vocal expressions produced by adult rhesus monkeys revealed strong evidence of a timing asymmetry (Table 3). Of 350 exemplars, 334 were asymmetric ($P < 0.0001$). More specifically, when producing barks, coos, copulation screams, grunts, girneys, harmonic arches, pant threats and screams, adults initiated these expressions with either the left or right side leading.

Table 3. Tests of whether rhesus vocal expressions are significantly more asymmetrical than symmetrical

Expression	Age	Number of individuals	Number of expressions		Sign test <i>P</i>	Mean asymmetry index	<i>t</i> (<i>df</i>)	<i>P</i>
			Asymmetric	Symmetric				
All expressions	Adult	35	334	16	0.0001	0.89	25.64 (34)	0.0001
Bark	Adult	28	93	4	0.0001	0.95	27.53 (7)	0.0001
Coo	Adult	20	69	3	0.0001	0.88	11.57 (8)	0.0001
Copulation scream	Adult	5	15	2	0.002	0.80*	(1)	—
Grunt	Adult	8	26	1	0.0001	1.0*	(1)	—
Girney	Adult	5	23	1	0.0001	0.89*	(2)	—
Harmonic arch	Adult	6	20	0	0.0001	1.0*	(2)	—
Pant threat	Adult	21	41	3	0.0001	0.67	(1)	—
Scream	Adult	9	47	2	0.0001	0.85	7.72 (5)	0.0006
All expressions	Juvenile	9	30	4	0.0001	—	—	—
Coo	Juvenile	7	17	2	0.0007	—	—	—
Scream	Juvenile	6	13	2	0.007	—	—	—
All expressions	Infant	38	104	7	0.0001	0.96	9.99 (4)	0.0001
Coo	Infant	25	45	6	0.0001	1.0*	(1)	—
Gecker	Infant	6	12	0	0.0005	1.0*	(1)	—
Grunt	Infant	6	9	0	0.004	—	—	—
Scream	Infant	10	25	1	0.0001	0.86*	(1)	—

*Sample too small for statistical testing.

Table 4. Tests of whether rhesus facial expressions are more asymmetrical to the left or to the right

Expression	Age	Number of individuals	Number of expressions		Sign test <i>P</i>	Mean asymmetry index	<i>t</i> (<i>df</i>)	<i>P</i>
			Right	Left				
All expressions	Adult	31	40	127	0.0001	0.70	5.76 (17)	0.0001
Copulation grimace	Adult	7	2	11	0.02	0.78*	(1)	—
Fear grimace	Adult	16	6	19	0.01	1.0*	(3)	—
Lip smack	Adult	15	21	50	0.0008	0.52	2.35 (8)	0.04
Open-mouth threat	Adult	26	11	47	0.0001	0.77*	(3)	—
All expressions	Infant	13	21	31	NS	0.38*	(3)	—
Fear grimace	Infant	9	3	12	NS	1.0*	(1)	—
Lip smack	Infant	5	11	12	NS	-0.04*	(1)	—
Play face	Infant	6	7	9	NS	0.18*	(1)	—

*Sample too small for statistical testing.

At the individual level, all vocal expressions showed asymmetries as measured by the asymmetry index, and for barks, coos and screams, this directional bias was statistically significant.

Like adults, juveniles and infants also consistently produced vocal expressions with a right or left side timing bias (Table 3). Specifically, juvenile coos and screams were produced with either the left or right side leading. Similarly, infant coos, geckers, grunts and screams were produced with either the left or right side leading. Sample sizes for juveniles and infants were insufficient to examine the statistical significance of the asymmetry index at the individual level.

Are Rhesus Facial Asymmetries Left or Right Biased?

Analyses of four facial expressions produced by adult rhesus monkeys revealed strong evidence of a left side timing asymmetry (Table 4). Specifically, when producing copulation grimaces, fear grimaces, lip smacks and

open-mouth threats, adults initiated these expressions with the left side leading. This pattern also emerged at the individual level, although it was only possible to test for statistical significance with lip smacks.

If one accepts the claim that copulation grimaces are associated with positive emotion, while fear grimaces, lip smacks, and open-mouth threats are associated with negative emotion, then our timing analyses provide no support for the emotional valence hypothesis. More specifically, it appears that for adult rhesus monkeys, the right hemisphere is dominant with respect to the timing of all facial expressions, independently of their emotional valence. Of course, if copulation grimaces turn out to be associated with negative emotion, then the pattern obtained would be consistent with the emotional valence hypothesis.

In contrast with adults, infants showed no evidence of a directional bias with respect to timing (Table 4). At present, it is difficult to determine whether the lack of a significant directional bias is due to a lack of a directional hemispheric bias prior to 1 year of age, variability in the

Table 5. Tests of whether rhesus vocal expressions are more asymmetrical to the left or to the right

Expression	Age	Number of individuals	Number of expressions		Sign test <i>P</i>	Mean asymmetry index	<i>t</i> (<i>df</i>)	<i>P</i>
			Right	Left				
All expressions	Adult	46	122	211	0.0001	0.30	2.26 (34)	0.03
Bark	Adult	28	38	55	NS	-0.23	-0.80 (7)	NS
Coo	Adult	20	23	46	0.008	0.61	2.64 (8)	0.03
Copulation scream	Adult	5	2	13	0.007	1.0*	(1)	—
Grunt	Adult	8	12	14	NS	-0.19*	(1)	—
Girney	Adult	5	9	14	NS	-0.02*	(2)	—
Harmonic arch	Adult	6	1	19	0.0001	0.90*	(2)	—
Pant threat	Adult	20	14	26	NS	0.67*	(1)	—
Scream	Adult	9	23	24	NS	0.72	3.07 (5)	0.03
All expressions	Juvenile	9	14	16	NS	—	—	—
Coo	Juvenile	7	7	10	NS	—	—	—
Scream	Juvenile	6	7	6	NS	—	—	—
All expressions	Infant	29	26	65	0.0001	0.86	9.99 (4)	0.006
Coo	Infant	25	15	30	0.04	0.8*	(1)	—
Gecker	Infant	6	2	10	0.04	1.0*	(1)	—
Grunt	Infant	6	2	7	NS	—	—	—
Scream	Infant	10	7	18	0.04	0.86*	(1)	—

*Sample too small for statistical testing.

ages represented in our sample, or the relatively small sample of exemplars and individuals per expression type. If hemispheric asymmetries for facial expression emerge at around 1 year, then our sample of infants, ranging in age from 6–12 months, would potentially obscure this effect.

Are Rhesus Vocal Asymmetries Left or Right Biased?

Analyses of asymmetry in the timing of adult vocal expressions revealed far greater variability than those of adult facial expressions (Table 5). In all cases where a statistically significant asymmetry was obtained, however, the bias was to the left; this was true at both the exemplar and individual level. Thus, at the exemplar level, adult rhesus monkeys showed a statistically significant left side bias for coos, copulation screams, harmonic arches and screams. At the individual level, there were significant left side biases for coos and screams.

The emotional valence hypothesis predicts that barks, pant threats and screams should be associated with a left side of the face bias, whereas coos, copulation screams, grunts, girneys and harmonic arches should be associated with a right side of the face bias. The results do not support this prediction. The approach–withdrawal distinction also fails to account for the pattern of results obtained. Coos, copulation screams, harmonic arches and pant threats are all associated with approach, and yet the directional bias was opposite from the predicted right side of the face bias.

In contrast with adults, juveniles showed no evidence of a statistically significant, directional bias. For coos and screams, some individuals showed a bias to the left, and some to the right. At the exemplar level, infants showed significant left side biases for coos, geckers and screams, but no significant bias for grunts; statistical analyses were

not possible at the individual level. Given that coos are associated with positive/approach, geckers with negative/approach, and screams with negative/withdrawal, the left side bias provides no support for the emotional valence hypothesis.

DISCUSSION

The goal of this paper was to assess whether rhesus monkeys show evidence of directional asymmetries in the timing of facial and vocal expressions, to explore whether asymmetries change over the course of development, and to assess whether there are differences between facial and vocal expressions. Results showed that all age classes produced facial and vocal expressions that were significantly asymmetric with respect to timing. The direction of this asymmetry was generally biased to the left side of the face, thereby implicating right hemisphere dominance. In terms of developmental change, juveniles showed no directional bias, while infants showed either a left side of the face bias or no consistent directional bias. Although changes in brain organization do occur after the first year of life, we think that a more likely explanation for the lack of an effect in juveniles is the small sample of subjects and expression types. In general, infants showed no evidence of a statistically significant directional bias for facial expressions, but showed a significant left side of the face bias for three out of the four vocal expressions. These data suggest that the hemispheric asymmetries underlying the production of facial expressions may develop more slowly than the asymmetries underlying vocal expression. Why there should be a difference in developmental timing between facial and vocal expression is currently unclear.

The emotional valence hypothesis, originally proposed for humans (reviewed in Davidson 1995, 1999), and recently supported by some animal studies (e.g. Hopkins & Bennett 1994; Hook-Castigan & Rogers 1998), was not

supported in the present study. In particular, for those expressions showing significant directional biases, some were associated with negative/withdrawal emotions and some with positive/approach emotions. All expressions with a significant directional bias, however, showed a left side of the face timing asymmetry. Similarly, there was no support for the hypothesis that functionally referential vocal signals show different patterns of asymmetry from vocalizations that convey more affective information.

At present, it is unclear why [Hook-Castigan & Rogers \(1998\)](#) found support for the emotional valence hypothesis in marmosets, whereas our investigation of rhesus did not. There are, however, several possible explanations for this apparent species difference. First, differences in brain structure between these species could underlie the observed differences in vocal expression. At present, although we know a great deal about the circuitry underlying emotion in rhesus monkeys, we know relatively little about marmosets ([Aggleton et al. 1981](#); [Amaral et al. 1992](#); [Dias et al. 1996](#); [Rolls 1999](#)). Until such comparative data are obtained, we cannot evaluate this explanation. Second, while the marmoset work presents results from one facial expression and two call types, from a small sample of subjects, work on rhesus monkeys presents results from a large sample of subjects, and includes eight call types and four facial expressions. It is thus unclear whether the pattern obtained for marmosets will generalize to a larger sample of subjects tested on both the same and different call types, as well as to an analysis of different facial and vocal expressions.

An interesting result to emerge from these findings is the contrast between vocal production and vocal perception. In work by Hauser and colleagues ([Hauser & Andersson 1994](#); [Hauser et al. 1998](#)), playback experiments revealed a significant right ear bias in adults for orienting to conspecific calls, but no orienting bias in infants. This pattern was robust, and consistent across all call types. Together with data from laboratory studies of rhesus and Japanese macaques ([Petersen et al. 1978](#); [Heffner & Heffner 1984](#); C. LePrell, M. D. Hauser & D. Moody, unpublished data), we have interpreted the orienting bias as evidence of a left hemisphere specialization for processing conspecific vocalizations. In contrast, in the present study adult rhesus monkeys tended to show a right hemisphere/left side of the face bias for producing vocalizations, as did infants. These results raise two hypotheses, one concerning differences in hemispheric specialization as a function of production versus perception mechanisms, the second concerning the development of such mechanisms.

In humans, the production and perception mechanisms underlying speech are both lateralized to the left hemisphere in a high percentage of right handers and in a strong majority of left handers ([Kosslyn et al. 1999](#)). In rhesus, it appears that the facial/motor control system is lateralized to the right hemisphere, the vocal perception system to the left hemisphere, and the hand motor control system to the right hemisphere ([Hauser et al. 1991](#)). If this characterization is correct, it suggests that an important change in brain organization occurred during the evolutionary transition from Old

World monkeys to humans. This hypothesis must be tested with additional data on rhesus monkeys, as well as additional studies of other species, especially the great apes.

Although we still need more data on infants, the current results suggest that the production system for vocal communication is lateralized quite early in life, whereas the perceptual system requires 1 year or more to become lateralized. This makes sense if the production of vocalizations is mediated by a mechanism that requires relatively little experiential input, whereas the perception of vocalizations, and specifically, the recognition of vocalizations as having specific informational importance (e.g. conspecific, alarm, food, etc.), develops as a function of considerable experiential input. Current studies of vocal learning in primates support this conclusion (reviewed in [Hauser 1996](#); [Seyfarth & Cheney 1997](#)). Based on observations and experiments, it appears that nonhuman primates are born with the ability to produce species-typical, acoustically appropriate vocalizations; experience plays little to no role in shaping the ontogeny of a call's acoustic morphology. In contrast, research on vocal comprehension suggests that nonhuman primates require a year or more to respond appropriately to vocalizations in their species-typical repertoire. Our timing asymmetry data add to these results, suggesting that the directional bias seen in adult vocal expressions is also seen in infants. In contrast, infants fail to show the directional bias that adults show while perceiving vocalizations.

In conclusion, these data add to the growing literature on lateralization in nonhuman animals ([MacNeilage 1991](#); [Bradshaw & Rogers 1993](#); [Vauclair et al. 1993](#); [Ward & Hopkins 1993](#); [Hopkins & Bard 1995](#); [Bisazza et al. 1998](#); [Hook-Castigan & Rogers 1998](#); [Hauser 1999](#); [Suthers 1999](#)). Not only do animals show asymmetries in hand preferences and detour behaviour, but they also show asymmetries in motor actions related to social interactions. Future work will explore other aspects of such production asymmetries.

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References

- Adolphs, R.** 1999. Neural systems for recognizing emotions in humans. In: *The Design of Animal Communication* (Ed. by M. D. Hauser & M. Konishi), pp. 187–212. Cambridge, Massachusetts: MIT Press.

- Aggleton, J. P., Burton, M. J. & Passingham, R. E. 1981. Cortical and subcortical afferents to the amygdala in monkeys (*Macaca mulatta*). *Brain Research*, **190**, 347–368.
- Amaral, D. G., Price, J. L., Pitkanen, A. & Carmichael, S. T. 1992. Anatomical organization of the primate amygdaloid complex. In: *The Amygdala* (Ed. by J. P. Aggleton), pp. 1–66. New York: J. Wiley.
- Bisazza, A., Rogers, L. J. & Vallortigara, G. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles, and amphibians. *Neuroscience and Biobehavioral Review*, **22**, 411–426.
- Blair, R. J. R., Morris, J. S., Frith, C. D., Perrett, D. I. & Dolan, R. J. 1999. Dissociable neural responses to facial expressions of sadness and anger. *Brain*, **122**, 883–893.
- Borod, J. 1993. Cerebral mechanisms underlying facial, prosodic and lexical emotional expression: a review of neuropsychological studies and methodological issues. *Neuropsychology*, **7**, 445–463.
- Bradshaw, J. L. & Rogers, L. 1993. *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect*. San Diego: Academic Press.
- Cantalupo, C., Bisazza, A. & Vallortigara, G. 1995. Lateralization of predator-evasion response in teleost fish. *Neuropsychologia*, **33**, 1637–1646.
- Cantalupo, C., Bisazza, A. & Vallortigara, G. 1996. Lateralization of displays during aggressive and courtship behaviour in the siamese fighting fish (*Betta splendens*). *Physiology and Behavior*, **60**, 249–252.
- Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: Chicago University Press.
- Cohen, J. A. 1960. Coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, **20**, 37–46.
- Darwin, C. 1872. *The Expression of the Emotions in Man and Animals*. London: J. Murray.
- Davidson, R. J. 1995. Cerebral asymmetry, emotion, and affective style. In: *Brain Asymmetry* (Ed. by R. J. Davidson & K. Hugdahl), pp. 361–389. Cambridge, Massachusetts: MIT Press.
- Davidson, R. J. 1999. The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Science*, **3**, 11–21.
- Davidson, R. J. & Hugdahl, K. 1995. *Brain Asymmetry*. Cambridge, Massachusetts: MIT Press.
- Dias, R., Robbins, T. W. & Roberts, A. C. 1996. Dissociation in prefrontal cortex of affective and attentional shifts. *Nature*, **380**, 69–72.
- Fischer, J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, **55**, 799–807.
- Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**, 1213–1222.
- Fitch, W. T. & Hauser, M. D. 1995. Vocal production in nonhuman primates: acoustics, physiology and functional constraints on honest advertisement. *American Journal of Primatology*, **37**, 191–219.
- Fleiss, J. L. 1981. *Statistical Methods for Rates and Proportions*. New York: J. Wiley.
- Floody, O. R. & Arnold, A. P. 1997. Song lateralization in the zebra finch. *Hormones and Behavior*, **31**, 25–34.
- Gainotti, G. 1972. Emotional behavior and hemispheric side of lesion. *Cortex*, **8**, 41–55.
- Gazzaniga, M. & Smiley, C. S. 1991. Hemispheric mechanisms controlling voluntary and spontaneous facial expressions. *Journal of Cognitive Neuroscience*, **2**, 239–245.
- Goller, F. & Suthers, R. A. 1995. Implications for lateralization of bird song from unilateral gating of bilateral motor patterns. *Nature*, **373**, 63–65.
- Gouzoules, S., Gouzoules, H. & Marler, P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, **32**, 182–193.
- Graves, R. & Landis, T. 1985. Hemispheric control of speech expression in aphasia: a mouth asymmetry study. *Archives of Neurology*, **42**, 249–251.
- Graves, R. & Landis, T. 1990. Asymmetry in mouth opening during different speech tasks. *International Journal of Psychiatry*, **25**, 179–189.
- Graves, R., Goodglass, H. & Landis, T. 1982. Mouth asymmetry during spontaneous speech. *Neuropsychologia*, **20**, 371–381.
- Graves, R., Strauss, E. H. & Wada, J. 1990. Mouth asymmetry during speech of epileptic patients who have undergone corotid amygdal testing. *Neuropsychologia*, **28**, 1117–1121.
- Graves, R. E. & Potter, S. M. 1988. Speaking from two sides of the mouth. *Visible Language*, **22**, 129–137.
- Hamilton, C. R. & Vermeire, B. A. 1988. Complementary hemispheric specialization in monkeys. *Science*, **242**, 1691–1694.
- Hamilton, C. R. & Vermeire, B. A. 1991. Functional lateralization in monkeys. In: *Cerebral Lateralization: Theory and Research* (Ed. by F. L. Kitterle), pp. 19–34. Hillsdale, New Jersey: L. Erlbaum.
- Hauser, M. D. 1992. Articulatory and social factors influence the acoustic structure of rhesus monkey vocalizations: a learned mode of production? *Journal of the Acoustical Society of America*, **91**, 2175–2179.
- Hauser, M. D. 1993a. Rhesus monkey (*Macaca mulatta*) copulation calls: honest signals for female choice? *Proceedings of the Royal Society, London, Series B*, **254**, 93–96.
- Hauser, M. D. 1993b. Right hemisphere dominance for the production of facial expression in monkeys. *Science*, **261**, 475–477.
- Hauser, M. D. 1993c. The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight and motivational state. *American Naturalist*, **142**, 528–542.
- Hauser, M. D. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.
- Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, **55**, 1647–1658.
- Hauser, M. D. 1999. The evolution of a lopsided brain: asymmetries underlying facial and vocal expressions in nonhuman primates. In: *The Design of Animal Communication* (Ed. by M. D. Hauser & M. Konishi), pp. 597–628. Cambridge, Massachusetts: MIT Press.
- Hauser, M. D. & Andersson, K. 1994. Left hemisphere dominance for processing vocalizations in adult, but not infant rhesus monkeys: field experiments. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 3946–3948.
- Hauser, M. D. & Marler, P. 1993. Food-associated calls in rhesus macaques (*Macaca mulatta*). II. Costs and benefits of call production and suppression. *Behavioral Ecology*, **4**, 206–212.
- Hauser, M. D. & Schön Ybarra, M. 1994. The role of lip configuration in monkey vocalizations: experiments using xylocaine as a nerve block. *Brain and Language*, **46**, 232–244.
- Hauser, M. D., Perry, S., Manson, J., Ball, H., Williams, M., Pearson, E. & Berard, J. 1991. It's all in the hands of the beholder: new data on handedness in a free-ranging population of rhesus macaques. *Behavioral and Brain Sciences*, **14**, 342–344.
- Hauser, M. D., Evans, C. S. & Marler, P. 1993. The role of articulation in the production of rhesus monkey (*Macaca mulatta*) vocalizations. *Animal Behaviour*, **45**, 423–433.
- Hauser, M. D., Agnetta, B. & Perez, C. 1998. Orienting asymmetries in rhesus monkeys: the effect of time-domain changes on acoustic perception. *Animal Behaviour*, **56**, 41–47.
- Heffner, H. E. & Heffner, R. S. 1984. Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science*, **226**, 75–76.
- Hook-Castigan, M. & Rogers, L. J. 1998. Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia*, **36**, 1265–1273.

- Hopkins, W. D. & Bard, K. A. 1995. Evidence of asymmetries in spontaneous head turning in infant chimpanzees (*Pan troglodytes*). *Behavioral Neuroscience*, **110**, 1212–1215.
- Hopkins, W. D. & Bennett, A. J. 1994. Handedness and approach-avoidance behavior in chimpanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, **20**, 413–418.
- MacNeilage, P. F. 1991. The “postural origins” theory of primate neurobiological asymmetries. In: *Biological Foundations of Language Development* (Ed. by N. Krasnegor, D. Rumbaugh, M. Studdert-Kennedy & R. Schiefelbusch), pp. 165–188. Hillsdale, New Jersey: L. Erlbaum.
- Marler, P., Evans, C. S. & Hauser, M. D. 1992. Animal signals? Reference, motivation or both? In: *Nonverbal Vocal Communication: Comparative and Developmental Approaches* (Ed. by H. Papoušek, U. Jürgens & M. Papoušek), pp. 66–86. Cambridge: Cambridge University Press.
- Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some birds and mammal sounds. *American Naturalist*, **111**, 855–869.
- Nottebohm, F. & Nottebohm, M. E. 1976. Left hypoglossal dominance in the control of canary and white-crowned sparrow song. *Journal of Comparative Physiology A*, **108**, 171–192.
- Owren, M. J. & Bernacki, R. 1988. The acoustic features of vervet monkey (*Cercopithecus aethiops*) alarm calls. *Journal of the Acoustical Society of America*, **83**, 1927–1935.
- Perrett, D. I., Mistlin, A. J., Chitty, A. J., Smith, P. A., Potter, D. D., Broennimann, R. & Haries, M. 1988. Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behavioural Brain Research*, **29**, 245–258.
- Petersen, M. R., Beecher, M. D., Zoloth, S. R., Moody, D. B. & Stebbins, W. C. 1978. Neural lateralization of species-specific vocalizations by Japanese macaques. *Science*, **202**, 324–326.
- Preuschoft, S. 1995. *‘Laughter’ and ‘Smiling’ in Macaques: an Evolutionary Approach*. Utrecht: University of Utrecht Press.
- Rawlins, R. & Kessler, M. 1987. *The Cayo Santiago Macaques*. New York: SUNY University Press.
- Rendall, D., Rodman, P. S. & Edmond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.
- Rendall, D., Owren, M. J. & Rodman, P. S. 1998. The role of vocal tract filtering in identity cueing in rhesus monkeys (*Macaca mulatta*) vocalizations. *Journal of the Acoustical Society of America*, **103**, 602–614.
- Rolls, E. T. 1999. *The Brain and Emotion*. Oxford: Oxford University Press.
- Rowell, T. E. & Hinde, R. A. 1962. Vocal communication by the rhesus monkey (*Macaca mulatta*). *Symposium of the Zoological Society of London*, **8**, 91–96.
- Sackeim, H. A. 1982. Pathological laughter and crying: functional brain asymmetry in the expression of positive and negative emotions. *Archives of Neurology*, **39**, 210–218.
- Sackeim, H. A., Gur, R. C. & Saucy, M. C. 1978. Emotions are expressed more intensely on the left side of the face. *Science*, **202**, 434–436.
- Seyfarth, R. M. & Cheney, D. L. 1997. Some general features of vocal development in nonhuman primates. In: *Social Influences on Vocal Development* (Ed. by C. T. Snowdon & M. Hausberger), pp. 249–273. Cambridge: Cambridge University Press.
- Suthers, R. A. 1999. The motor basis of vocal performance in songbirds. In: *The Design of Animal Communication* (Ed. by M. D. Hauser & M. Konishi), pp. 37–62. Cambridge, Massachusetts: MIT Press.
- Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G. & Robins, A. 1998. Complimentary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport*, **9**, 3341–3344.
- Vallortigara, G., Regolin, L. & Pagni, P. 1999. Detour behaviour, imprinting and visual lateralization in the domestic chick. *Brain Research*, **7**, 307–320.
- Vauclair, J., Fagot, J. & Hopkins, W. 1993. Mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychological Science*, **4**, 99–103.
- Vermeire, B. A. & Hamilton, C. R. 1998. Inversion effect for faces in split-brain monkeys. *Neuropsychologia*, **36**, 1003–1014.
- Ward, J. P. & Hopkins, W. D. 1993. *Primate Laterality: Current Behavioral Evidence of Primate Asymmetries*. Berlin: Springer-Verlag.