

On the Genetics and Measurement of Human Handedness

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Lateral preferences in humans and other primates may be a key to many important issues in biology and psychology. There is strong evidence that the representation of language functions in the cerebral cortex is different in left-handed (LH) people than in right-handed (RH) people, and an understanding of handedness may lead to valuable clues as to how the brain becomes organised in the way that it does. Although there are clearly cultural effects that influence manual activities, there is nevertheless evidence that human handedness and other lateralities are at least in part genetically determined: compared with two RH parents, one RH and one LH parent are 2-3 times more likely to have an LH child, and two LH parents are 3-4 times more likely to have an LH child. Thus, one might wish to investigate the genetics of laterality with the goal of understanding the biological mechanisms that lead to the preferential use of one hand (or eye or foot). One may also see links between human handedness and footedness and the motor asymmetries found in many nonhuman primate species, and perhaps in lower mammals as well. From this perspective, one might see the study of human laterality as relevant to evolutionary biology. Investigators of both human and nonhuman asymmetries have to grapple with such difficult measurement issues as the relations between

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[†] Phil Bryden died suddenly in August 1996, shortly after the joint meetings of the International Primatological Society and the American Society of Primatologists in Madison, Wisconsin, where he made a presentation on which this paper is based.

preference and performance, and the influences of postural and task demands, and have much to offer each other in the quest for the nature of laterality. Our recent work seems to indicate that the various sensory and motor lateralities may be related, in humans, but not in a simple way. In future work, the challenge will be to identify the relations between the various laterality "profiles" and patterns of functional cerebral organisation.

INTRODUCTION

This manuscript is based on the Bryden and Roy paper, which Phil Bryden presented at the joint meetings of the International Primatological Society and the American Society of Primatologists in Madison, Wisconsin, in August of 1996 very shortly before his premature death. In it, we review some of our recent collaborative work involving cultural and genetic influences on handedness, and discuss performance measures of handedness as well as the effects of task and postural demands on handedness measurement. Finally, we discuss the relations of lateral preferences to brain organisation and suggest some possibly fertile areas for further investigation.

It is obvious that some of our manual activities are heavily influenced by the society in which we live. For example, some studies in which handedness has been used as a factor have determined handedness by the response to two questions: "Which hand do you write with?" and "In which hand do you hold a fork when eating?". The response to the first question is quite straightforward, whereas that to the second is influenced by the respondent's cultural experience. Transferring the fork to the preferred hand is an American custom, whereas the European style is to keep the fork in the left hand. This observation reflects the importance of considering cultural differences in hand usage before one can offer a general method of assessing human handedness.

In recent years, we have had the opportunity to administer handedness questionnaires in Canada, India, Japan, and among the Tucano, an aboriginal people in the Amazon watershed of Colombia (Bryden, Ardila, & Ardila, 1993; Ida & Bryden, 1996; Singh & Bryden, 1994; Steenhuis & Bryden, 1989b). Common lore has it that lefthandedness is discouraged in the Orient, and so it should not be particularly surprising to note that left-handedness is less common in India and Japan than it is in Canada (see Table 1). One might also note that left-hand preference is a rarity among the Tucano. Although some Tucano carry out some activities with the left hand, we have yet to find anyone whom we would classify as even moderately LH. Similar data in other aboriginal peoples have been reported by Marchant, McGrew, and Eibl-Eibesfeldt (1995). A second point is that left-hand usage is more frequent for relatively unskilled activities, such as dusting or picking up small objects, than it is for more skilled activities such as writing or throwing.

The obvious interpretation of these data is that hand preference is heavily influenced by the culture in which one lives, and certainly there are strong

TABLE 1
Prevalence of Left-handedness for Selected Hand Preference Items (%)

Item	Canada 1563 ¹	India 2104	Japan 655	Tucano 65
Write	9.81 ²	5.19	1.37	0.00
Toothbrush	8.27	6.04	7.43	
Strike match	8.77	6.67	3.92	1.54
Throw dart/spear	10.55	7.16	4.58	0.00
Comb hair	14.09	6.79	5.14	0.00
Pick up object	9.70	10.79	3.00	1.54
Carry suitcase	14.26	8.08	17.17	7.69
Dust	15.81	9.65	7.29	
Mean	11.41	7.55	6.23	1.81
Mean skilled	9.35	6.27	4.32	0.55
Mean unskilled	13.47	8.83	8.14	3.07

¹ Number in the sample.

² Percent.

proponents of such a view (e.g. Harris, 1990; Porac, Rees, & Buller, 1990). On the other hand, if handedness is genetically controlled, it is entirely possible that the gene that leads to left handedness is less common in particular biological subgroups. Most certainly this is true for the genes responsible for such things as A-B-O blood type, as has been so elegantly shown by Cavalli-Sforza, Merrozz, and Piazza (1994) in their book on the geography of human genes. Likewise, we (McManus & Bryden, 1993) have argued that the lack of lefthandedness among the residents of the South Atlantic island of Tristan da Cunha may have arisen simply because the relevant gene is not present in the population, having disappeared as a result of a combination of founder effects, evolutionary bottlenecks, and random drift¹.

ON THE GENETICS OF HANDEDNESS

At present, there are at least three reasonable genetic models of handedness: Those of Annett (1985a); McManus (1985c; McManus & Bryden, 1992); and Yeo and Gangstad (1993). The Annett and McManus models are both single-

¹ It should be noted that the same mechanism cannot produce occasional populations in which everyone is left-handed, because the CC genotype (see the next section for an explanation of the handedness model on which we base this argument) only allows fluctuating asymmetry (i.e. 50% left-handedness and 50% right-handedness). It is also highly unlikely that the C allele rather than the D allele ever goes to fixation in small isolated populations, because a far lower proportion of the initial gene pool consists of C alleles in the first place.

gene models. Essentially, they propose that one allele codes for right-handedness (and left-hemisphere language dominance) while a second allele leaves the determination of lateralisation to fluctuating asymmetry. In contrast, Yeo and Gangestad have proposed a polygenic model in which both left-handedness and strong right-handedness are seen as deviations from the norm of moderate right-handedness. Although the genetics of their model have not been specified in detail, they have shown that strongly RH people, as well as left-handers, have an elevated proportion of parents who are left-handers.

We have chosen the McManus (1985c) model to focus on here because it is relatively easy to explain. This model involves two alleles, D and C. Individuals with the DD genotype will be RH and left-lateralised for language. CC individuals will be lateralised by the chance mechanisms of fluctuating asymmetry, and therefore 50% will be LH and an independent 50% will be right-lateralised for language. The model is an additive one, and therefore in the heterozygotes one can imagine the result as the D allele being expressed in 50% of the genotype and the C allele being expressed in the other 50%. Thus, 25% of those with the DC genotype will be LH. Lest there is confusion, it should be emphasised that the McManus (1985c) model uses fluctuating asymmetry in a subtly different way from that of Yeo and Gangestad (1993), although both are referring to the same phenomenon. In both cases, small amounts of random noise mean that the two sides of an otherwise symmetric organism are not the same, and differences between the two sides are distributed with a mean of zero and a non-zero standard deviation. The McManus (1985c) model takes this case and adds canalisation to it, with the result that half of the population becomes "dominant" on one side and the other half "dominant" on the other side, with the specific result for the CC genotype that 50% become "RH" and 50% "LH".

Interested readers may also care to compare the McManus model with that of Annett (Annett, 1985a, 1995), which in its application to family and twin data is broadly similar to that of McManus, although there are differences in details, particularly with regard to phenotypics (Annett, 1985b; McManus, 1985a,b). Detailed statistical comparison of the two models finds evidence in favour of one (Annett, 1996) or the other (McManus, 1985c).

In recent years, we have carried out family studies in both India and Canada. In the past, most such family studies have relied on the members of a particular target population reporting on their handedness and that of their relatives. Our family studies differed from previous studies in three important ways. First, we employed a multi-item questionnaire, rather than basing our statements solely on writing hand; second, each participant in the study responded to the questionnaire rather than single target subjects indicating the handedness of their relatives; third, we administered a common series of 10 questions to

participants in Canada and India.² (See Table 1 for a summary of the prevalence of lefthandedness for selected hand preference items.)

Respondents assessed their hand preferences on a 5-point scale, ranging from "always use left hand" (-2), to "always use right hand" (+2), and responses were summed to obtain a hand preference score. Based on the total score, each subject was classified as being either LH or RH, and as strongly or weakly handed, based on the absolute value of the score's deviation from zero.

We obtained data from 208 nuclear families with 457 children in Canada and 475 families with 1071 children in India. The increase in left-handedness resulting from having at least one LH parent was determined by calculating an odds ratio.

For two RH parents, the odds of having an LH child are obtained by simply dividing the total number of LH children produced from such matings by the number of RH children resulting (e.g. if there are ten right-handed and one left-handed offspring the odds are 1:10 [or 10:1 against] or .1). For two parents at least one of whom is LH (this would include cases in which one parent is LH and one is RH as well as cases in which both parents are LH), the odds of having a left-handed child are calculated in a similar manner (say 1:5 or 5:1 against, or .2). If one then forms the ratio of these odds (the "at-least-one-LH-parent" case divided by the "two-RH-parents" case) one obtains the odds ratio. This, then, is a measure of the increased likelihood of LH children resulting from matings involving at least one LH parent. (In this case, .2 divided by .1 which gives a value of 2, or 2:1, so that LH parents are twice as likely to have an LH child as are RH parents.) This ratio is equal to 1 under the null hypothesis that the two types of matings result in equal numbers of LH children. One of the nice things about odds ratios is that, under the null hypothesis, the sampling distribution of the natural logarithm of the odds ratio is normal, has a mean of zero, and a known and easily obtained variance (provided the cell frequencies are sufficiently large), so one can use a simple *z*-score for significance testing (Marascuilo & Serlin, 1988).

Table 2 presents the parent-child odds ratios when respondents were classified as LH and RH. As can be seen from Table 2, in Canada, LH parents produce LH offspring about twice as often as do RH parents. In India, LH parents produce LH offspring about three times more often than do RH parents.

We also classified our subjects in two other ways. First, they were divided into strongly handed and weakly handed categories, disregarding direction of preference. Strongly handed people were those who claimed to always use their preferred hand for each of the activities we questioned, whereas weakly handed

² The ten items were: Which hand would you use to (1) write (2) hold a toothbrush (3) strike a match (4) throw a spear (5) comb your hair (6) pick up a small object (7) carry a heavy suitcase (8) dust (9) flip a coin (10) throw a ball?

TABLE 2
Odds-ratios¹ for Parent-Child Relations

	<i>Canada</i>	<i>India</i>
Direction (Left/Right)	2.09*	3.07*
Degree (Strong/Weak)	1.75*	5.13*
Extreme/Moderate	1.23	2.78*

* $P < .01$

¹ For the direction measure, this is the ratio of the odds of two parents, at least one of whom is left-handed, producing a left-handed child to the odds of two right-handed parents producing such a child. For the degree measure, it is the ratio of the odds of two parents, at least one of whom is strongly handed producing a strongly handed child, to the odds of two weakly handed parents producing a strongly handed child. For the extreme/moderate classification (based on the Yeo-Gangestad model, see text), it is the ratio of the odds of two parents, at least one of whose scores falls in either of the extreme quartiles of the hand preference distribution, producing a child with a similar score, to the odds of two parents whose scores fall in the interquartile range producing a child scoring in one of the extreme quartiles.

people were those who often said that they used both hands about equally or that they usually used the preferred hand. Interestingly, there are significant parent-child associations for degree of hand preference as well as for direction. In India, strongly handed parents are about five times more likely to produce strongly handed children than are weakly handed parents. In Canada, the relation holds only for fathers, and it is rather weaker than it is in India (see Table 2). This result is reminiscent of Collins' mouse studies, in which, although unsuccessful in his attempts to breed for direction of paw preference, he established two lines of mice that differed in their degrees of paw preference—the Collins HI and LO strains (see Collins, 1985, for a review). A recent large survey of genetically different inbred mouse strains by Biddle and his colleagues (Biddle & Eales, 1996) has revealed that strains fall into three classes based on degree of paw preference. These mouse studies may well provide the model system through which the biological underpinnings of human lateral asymmetries are uncovered (Carlier, 1995).

The extreme/moderate (Table 2) classification was done in an attempt to compare the McManus (1985c) and Yeo-Gangestad models. Yeo and Gangestad's model predicts that those parents who differ from the population norm of moderate righthandedness will be more likely to produce similarly deviant children than those who are closer to the population norm. We therefore divided the distribution of hand preference scores into quartiles, and classified those

people in the middle two quartiles as “moderate” and those in the outer two quartiles as “extreme”, and repeated our odds-ratio (OR) calculations. Although the extreme/moderate classification leads to significant effects in the Indian sample, the values for the Canadian sample fail to reach significance.³ In other words, in our data the Yeo–Gangestad model is not supported because, at least for the Canadian sample, a couple at least one of whom deviates from moderate right-handedness is no more likely to produce an “extremely” handed child than is a couple both of whom are “moderately” handed. These data would suggest that the McManus model is a better fit to the data than is the Yeo–Gangestad model (see Table 2).

In the McManus model, as the frequency of the C allele decreases, the OR for the parent–child association increases. Table 3 shows the proportions of LH offspring, in relation to the handedness of the parents, in three situations. Case A shows the model described by McManus (1985c) in which the C allele has a frequency of 0.155, DD, DC, and CC genotypes produce 0%, 25%, and 50% left-handers, respectively, and therefore the frequency of left-handedness in the population is 7.75%. Case B shows the situation in which the frequency of the C allele has fallen to .0775, but otherwise the model stays the same; now 3.88% of the population are LH. Case C keeps the same C allele frequency as in Case A, but instead the expression of left-handedness is less, being 0%, 12.5%, and 25% in genotypes DD, DC, and CC. In effect there is social pressure against being LH. The result is that again 3.88% of the population are LH, but note that the proportions of left-handers in the different types of family are different from Case B. Thus, although manipulations for cases B and C (see Table 3) both have the same effect on the overall prevalence of left-handedness, they have different effects on the pattern within families, meaning that such cross-cultural data can provide leverage on the question of whether the incidence of left-handedness differs among societies because of differences in gene frequency or because of differences in social pressures. The increased OR in the Indian populations observed in comparing Tables 2 and 3 provides strong evidence for a difference in gene frequency rather than a simple difference in social pressure, which would result in almost no change in the OR. To summarise, the differences between Canada and India are most parsimoniously explained by differences in the frequency of the C allele.

MEASUREMENT OF HAND PREFERENCE

In the family studies, we have made use of paper-and-pencil preference inventories, partially because it is easy to use such materials to test large numbers of subjects. Because different people may interpret the instructions on

³ The statistical significance of the ORs can be determined by evaluating the natural logarithm of the OR for significance (see Bryden, McManus, & Bulman-Fleming, 1994, for an example).

TABLE 3
Left-handedness in Relation to Handedness of Parents

	<i>Case A</i>	<i>Case B</i>	<i>Case C</i>
p(C)	.155	.0775	.155
p(L DD)	0	0	0
p(L DC)	.25	.25	.125
p(L CC)	.5	.5	.25
p(L)	.0775	.0388	.0388
p(L R × R)	.0598	.0295	.0345
p(L R × L)	.1743	.1494	.0894
p(L L × L)	.2888	.2694	.1444
Odds ratio ¹ (R × L vs. R × R)	3.32	5.79	2.75
Log (odds ratio)	1.200	1.756	1.011

Abbreviations: p(C), the frequency of the C allele in the McManus (1985c) model of handedness; p(L|DD), p(L|DC), p(L|CC), the probabilities of being left-handed, given DD, DC, and CC genotypes, respectively; p(L), the frequency of left-handedness in the population; p(L|R × R), p(L|R × L), p(L|L × L), the conditional probabilities of a child being left-handed given the handedness of the parents.

¹ The ratio of the odds of one left-handed and one right-handed parent producing a left-handed child, to the odds of two right-handed parents producing a left-handed child.

such questionnaires differently, we might be faulted for not employing more performance-based tasks. One problem is that a preference inventory allows one to ask about a variety of activities, whereas performance measures assess a single task. In general, performance on particular manual tasks correlates well with responses to the relevant questionnaire items (Steenhuis, 1996). For example, people who claim that they “always” throw with their right hand show a larger hand difference in throwing accuracy than those who claim that they “usually” throw with the right hand. Furthermore, there is no question that practice on a particular task with the nonpreferred hand can improve performance with that hand. Thus, it would be desirable to develop a general objective measure of hand preference.

A number of performance tests of handedness have been developed and popularised over the years, such as the Tapley and Bryden (1985) dot-filling task, Dorothy Bishop’s (1990) square-tracing task, and Marian Annett’s (1985a) peg-moving task. Although these measures yield reliable differences between the hands, they each measure a specific activity, and that activity may not be the most important one to measure. Van Horn, in London, has carried out a factor-analytic study of a number of variants of these performance measures, and found that each test loaded on a distinct factor (Van Horn, 1992). Barnsley and Rabinovitch (1970) have also shown that hand differences on different performance tests do not correlate very well. One is thus faced with the question of which performance test to choose.

It seems plausible that the difference between preferred and nonpreferred hands should be larger for complex tasks than for simple ones. There is little difference between the hands in our ability to pet a cat or wave goodbye although most of us will use the preferred hand for such activities more often than not. In contrast, there is a fairly large difference between the preferred and nonpreferred hands in the ability to throw a ball accurately or to write legibly. These differences are reflected in the responses to preference inventories. By and large, people tend to endorse the extreme categories on questions involving some skill, such as writing, throwing, and using a toothbrush, whereas they endorse more moderate categories on questions involving less skill, such as picking up small objects or petting animals (Steenhuis & Bryden, 1989a).

Thus, the preferred hand advantage is larger for handwriting than for grip strength (Provins & Magliaro, 1989), for aiming as opposed to tapping (Flowers, 1975), and for inserting pegs as opposed to removing them (Roy, Bryden, Bulman-Fleming & Roy, 1996). We have plotted the ratio of the time taken by the nonpreferred hand (NP) to that taken by the preferred hand (P) for a variety of different tasks examined in our laboratory on the same subjects. In one task, the Grooved Pegboard, subjects were asked to insert the 25 pegs and remove them. In another task, the Annett pegboard, various task dimensions were manipulated. One manipulation involved performing the standard task either seated or standing. Another manipulation involved varying the size of the pegs as a means of varying the spatial complexity (Fitts, 1954) of the peg-placing movements (Bryden, Roy, Bryden, Allard, Whitelaw, Bulman-Fleming, & Roy, 1997). The third task was the Tapley-Bryden (1985) dot-aiming task. Because the measure in all of these tasks is the time taken to perform the task with each hand, the value of this ratio will normally be greater than 1.00. An analysis of this NP/P ratio (see Fig. 1) reveals that it is very similar across the variants of these placing tasks, but that it does range from very small for removing pegs to very large for the Tapley-Bryden dots task. This analysis does raise the interesting possibility of using the slope of the NP/P function over a range of tasks as a measure of degree of handedness.

We have also carried out a more detailed kinematic analysis of the influence of task demands on manual asymmetries (Roy, *in press*). In this task subjects had to reach and pick up a small metal dowel. In one condition the dowel had to be placed into a small receptacle about the same size as the dowel or into a large receptacle, with the movement precision requirements being greater in the small place condition. The movement was examined in two phases, a reach (pick up the dowel) and a place phase. The effect of precision demands was seen only in the second phase of the task (move and place the object) as opposed to the first phase (reach and pick up the object). That is, there were no differences in movement time, peak speed, or time in deceleration between the small and large place tasks in picking up the dowel. In the second phase, however, when placing the dowel into the small receptacle subjects moved more slowly and spent more time in deceleration.

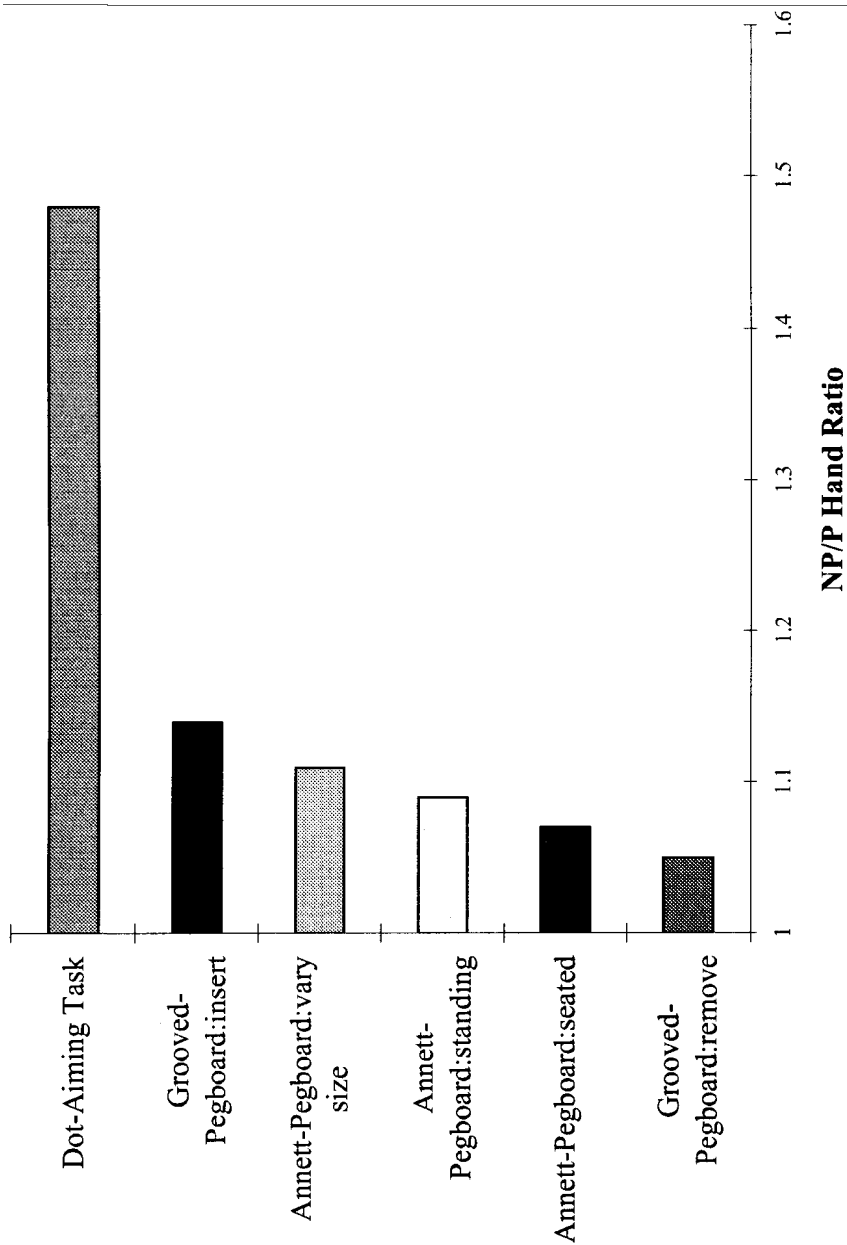


FIG. 1. Performance of the non-preferred relative to the preferred hand on various motor tasks.

We might interpret differences between these two conditions as reflecting differences in the skill required to perform the movement in the two phases of the task. That is, if a movement requires some degree of skill, it should be sensitive to the differences in the spatial precision demands of the two conditions. Using this interpretation, the absence of a difference between the conditions in the first phase reflects the relatively low skill required to pick up the dowel. The large difference in the second phase implies the higher level of skill demanded when moving and placing the dowel in the receptacle.

Analyses of the performance with each hand revealed a right- or preferred-hand advantage only in the second phase. The right hand moved with greater speed and spent less time in deceleration. The presence of a preferred-hand advantage only in the second phase appears related to the differences in skill demanded in the two phases, with this advantage appearing only in the more skilful second phase. This influence of the spatial precision demands or skill level on manual asymmetries in performance is consistent with Steenhuis and Bryden's (1989a) observations on hand preference. They found that skill was a factor in hand preference in that hand preferences were stronger for skilled than for unskilled activities. This link between preference and performance as it relates to task demands is examined more closely in our work on performance-based measures of preference.

One of the first measures developed to attempt to integrate measures of preference and performance was that of Bryden, Singh, Steenhuis, and Clarkson (1994). They had subjects seated at one end of a long pegboard, asked them to move pegs, leapfrog-style, from the near end to the far end, starting with the hand contralateral to the pegboard and shifting to the other hand whenever they elected to do so, and measured the point at which this shift occurred. Right-handers maintained the use of the right hand when moving leftward over a longer range than they used the left hand when moving rightward. Left-handers performed in the opposite manner.

The problem with this task is that it is quite transparent to the subject. Bryden and Edmonds (1995) developed a somewhat different task. Subjects were seated before a computer display terminal with control knobs below and on each side of the screen. When a light came on above one of the control knobs, subjects were to turn that control to adjust a cursor on the screen to a target. Although this study was ostensibly a study concerning the relation between knob location and turning behaviour, we observed which hand was used to turn the control knob. Left-handers were more likely to turn the lower knob (middle) with their left hands, whereas right-handers used their right hands. Furthermore, strongly handed people, as defined by a preference inventory, were far more likely to reach across the midline with their preferred hands than were weakly handed people. Thus, this task has the potential for providing an objective measure of hand preference, as opposed to hand skill. A similar task, involving picking up playing cards, has been developed by Bishop, Ross, Daniels, and Bright (1996).

Recently, we have examined the way in which task demands influence the hand that is used to carry out a task that is very similar to the Bryden and Edmonds (1995) task (Bryden, Roy, Bryden, Boucher, Pryde, & Frank, in press). Seven dowels were placed at 30° intervals from 90° to the left of the subject to 90° to the right. Subjects were then asked to carry out some action on these dowels. The various actions involved simply touching the dowel, knocking it over with a sweeping motion, picking it up and tossing it on the table, and picking it up and placing it in a small receptacle. Subjects crossed the midline with their preferred hands far more often than with their nonpreferred hands. Furthermore, as task complexity increased from touching to placing, the preferred hand encroached further into contralateral space. Although these findings show the same general pattern as reported by Bryden and Edmonds (1995) and by Bishop et al. (1996), they also indicate that the region of space in which the preferred hand is used is larger for complex actions than for simple ones. Thus, performance and preference are inextricably interwoven.

THE RELATION OF LATERAL PREFERENCES TO BRAIN ORGANISATION

Why should we be so interested in the measurement of handedness? We have long known that there is a weak but consistent relation between handedness and cerebral speech lateralisation (see Roy, 1996, for a discussion of praxis lateralisation and handedness). In the studies that support this conclusion, handedness has conventionally been determined by writing hand. Recently, we have also been investigating the lateralisation of throwing, kicking, and sighting, and have seen that they are interrelated in rather complex ways.

First of all, it is notable that writing hand and throwing hand are often not the same. Curiously, a relatively high proportion of LH writers throw with their right hands, whereas very few RH writers throw LH (Gilbert & Wysocki, 1992). This is a very different pattern from the one we would expect were the dissociation due to cultural pressure to write with the right hand, in which one would expect to find a large number of "natural" left-handers who had learned to write with the right hand but retained their left-hand preference for throwing. Furthermore, a cluster analysis of our handedness data indicated that left-handers split into two distinct groups, with about 70% throwing with the left hand and 30% throwing with the right hand (Grimshaw & Bryden, 1995).

We have also examined the association between handedness and the preferred eye for sighting. In the general population, about 65% of RH individuals sight with their right eyes, whereas only 43% of left-handers do (Bourassa, McManus, & Bryden, 1996). Thus, there is a relation between handedness and eyedness. When one separates writing hand and throwing hand, a somewhat clearer picture emerges. Of those who throw and write RH, about 75% are also right-eyed. Similarly, of those who throw and write LH, about 75% are left-eyed. It is those

who throw with one hand and write with the other who do not follow this pattern: about half are left-eyed and half are right-eyed (McManus, Porac, Bryden, & Boucher, 1997). These data suggest that writing hand and throwing hand contribute about equally as predictors of eye dominance.

These effects suggested to us that eyedness and throwing hand might prove to be better predictors of language lateralisation than writing hand, and we have found at least limited support for these ideas. To assess language lateralisation, we have used a noninvasive technique called dichotic listening, which involves the presentation of different words or syllables to the two ears at the same time. In dichotic listening, subjects normally show superior performance on the ear contralateral to the hemisphere specialised for language (Zatorre, 1989). Thus, most people show a right-ear advantage (REA) for identifying verbal material, because most humans are left-hemispheric for language.

Bryden (1988) reported dichotic-listening data from a CV-syllables task on a sample of 302 undergraduates who had been assessed for handedness, eyedness, and familial sinistrality. In this study handedness and eyedness were both related to the magnitude of the dichotic REA. Analyses of the difference in the percentage of left- and right-handers and in left- and right-eyed subjects showing an REA revealed that the eyedness effect is considerably smaller than the handedness effect, although it is clearly present (see Fig. 2).

The Fused Dichotic Words Test (FDWT), developed by Wexler and Halwes (1983), is a somewhat more valid measure of language lateralisation. By carefully aligning the stimuli, the two words fuse into a single percept, so that the listener is unaware of the fact that two different stimuli are being presented, yet a right-ear effect is still observed. Thus biases to attend to one ear in preference to the other do not affect performance. Zatorre (1989) has shown that performance on the FDWT is closely related to language lateralisation determined by unilateral sodium amytal suppression. Because of these properties, we have been using the FDWT in recent years.

Grimshaw and Bryden (1995) administered the FDWT to 155 participants who varied in their writing and throwing hands. Analyses of the percentage of those with an REA among right- and left-writers and right- and left-throwers (see Fig. 3) showed the writing-hand effect to be somewhat larger than it was in the earlier study with CV-syllables, reflecting the better measurement qualities of the FDWT. In addition, there was an independent effect of throwing hand of approximately the same magnitude. In a more recent study, again using the FDWT, Elias (1996) found throwing hand to be a better predictor of language lateralisation than writing hand: the correlation between throwing and the REA was .45 ($df = 30$, $P < .01$), whereas that between writing hand and the REA was only .22 ($P > .20$).

Because of numerous subtle hints in the literature (e.g. Searleman, 1980), we have recently completed a study in which we looked at handedness and footedness as predictors of the dichotic REA in the FDWT (Elias & Bryden, in

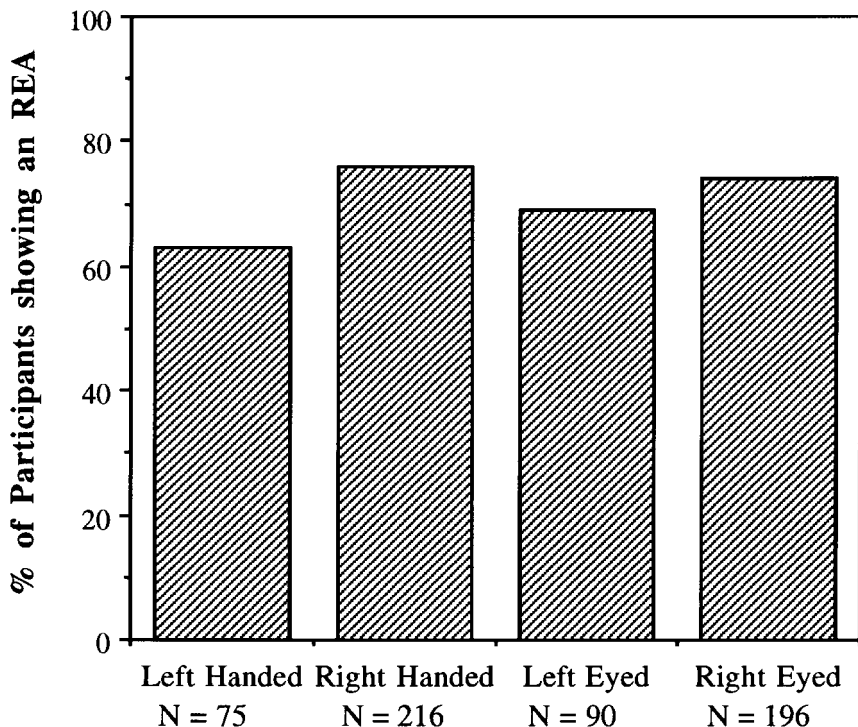


FIG. 2. The percentage of participants exhibiting a right-ear advantage on a dichotic-CV syllables task, classified according to handedness and eyedness (from Bryden, 1988). Because of missing data and the fact that some participants did not show an ear advantage, the total Ns for handedness and eyedness do not total 302, the number of participants in the study.

press). We recruited 32 participants half of whom were RH and half LH such that equal numbers of each group were left-footed and right-footed. These data (see Fig. 4 and Table 4) show that the handedness effect we have seen before is still present (although not significant because of the relatively small sample sizes), but the effect of footedness is very much larger. Similar data, using a different dichotic task, have been reported by Day and MacNeilage (1996). We have, even more recently, found evidence that footedness appears to also be a better predictor of the dichotic left-ear advantage (LEA) for the detection of the emotional content of words (Elias, Bryden, & Bulman-Fleming, in press).

The data from these three studies are summarised in Table 4. Here, we have shown the relative odds (the OR) for a right-sided person showing an REA rather than an LEA as opposed to a left-sided person showing that pattern. For example, in Bryden's 1988 study, a right-hander was 1.77 times more likely to show an REA than was a left-hander. These data indicate that footedness is by far the best predictor of the REA, with throwing and writing hands being

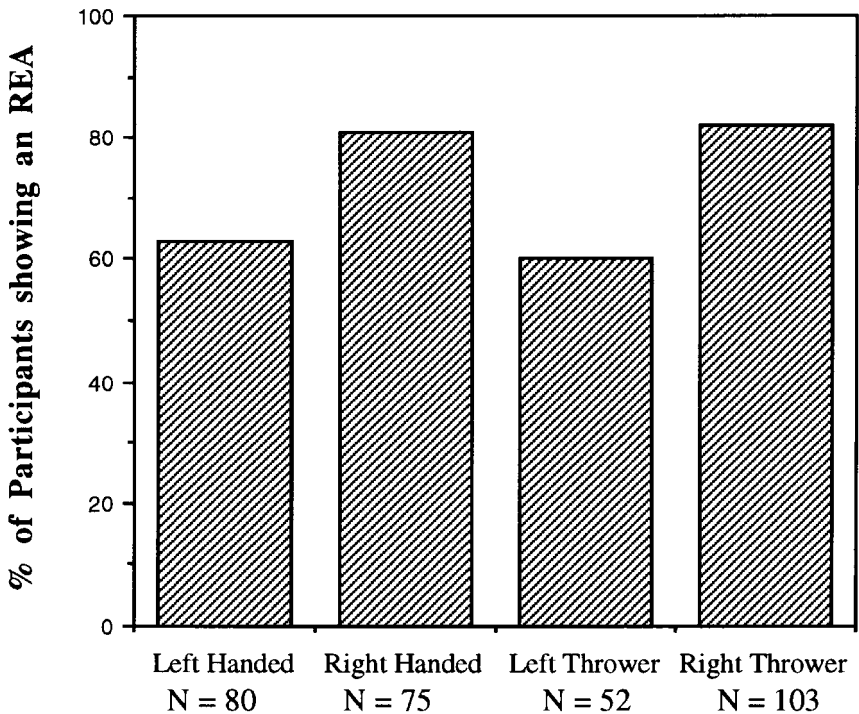


FIG. 3. The percentage of participants exhibiting a right-ear advantage on the Fused Dichotic Words Task, classified according to handedness and throwing hand (from Grimshaw & Bryden, 1995).

TABLE 4
Odds Ratios¹ Relating Laterality Variables to the Dichotic Right Ear Advantage (REA)

Bryden, 1988	Hand	1.77*	Eye	1.32
Grimshaw & Bryden, 1955	Hand	3.13**	Throw	2.90**
Elias & Bryden, in press	Hand	2.60	Foot	15.0*

* $P < .05$

** $P < .01$

¹ The ratio of the odds of a right-sided (handed, eyed, throwing hand, footed) person showing an REA (as opposed to an LEA) to those of a left-sided person showing an REA.

roughly equally important, and eyedness having but a small effect. The notion that footedness, rather better than preferred hand for writing, relates to cerebral organisation provides some support for the notion that language lateralisation is an evolutionary consequence of asymmetries in postural control (MacNeillage, 1991; Previc, 1991), although the specific aspects of “footedness” that we have

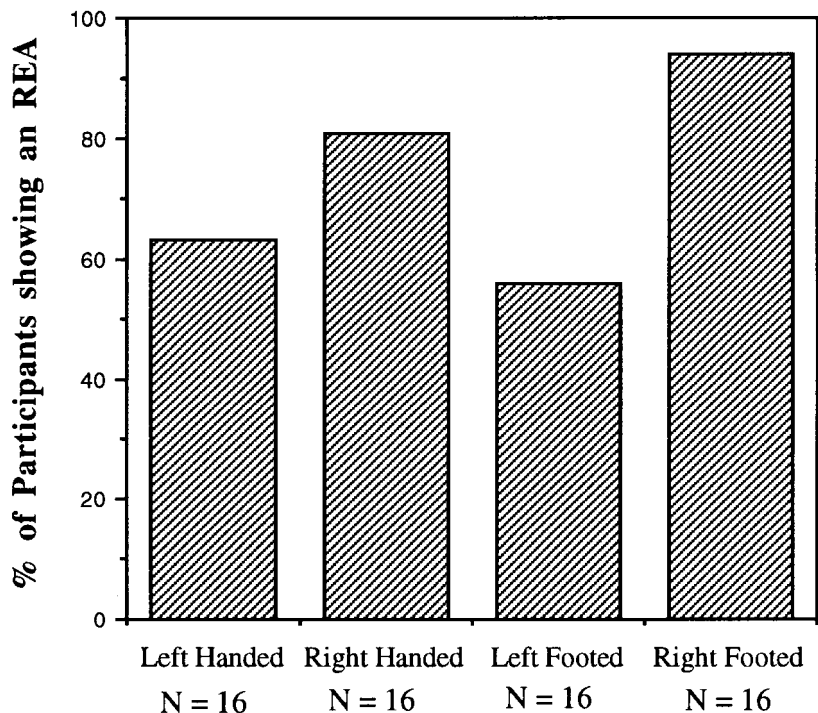


FIG. 4. The percentage of participants exhibiting a right-ear advantage on the Fused Dichotic Words Task, classified according to handedness and footedness (from Elias & Bryden, in press).

found to be predictive (the skilled or ballistic component) are not those that would support the MacNeilage (1991) model. The effect of throwing hand seen in the Grimshaw and Elias studies is reminiscent of Calvin's (1983) proposition that human handedness evolved from throwing stones at moving targets. Interestingly, Hopkins and his colleagues observed that a sample of captive chimpanzees preferentially threw right-handed when they were in a bipedal posture (Hopkins, Bard, Jones, & Bales, 1993).

The three studies we have just described were carried out at quite different times, when somewhat different issues were foremost. Our problem now is to determine how the four variables of eyedness, footedness, throwing hand, and writing hand interact to predict lateralisation of function.

CONCLUSIONS

What does all this have to do with primate handedness? Our data indicate that there is a significant genetic contribution to human handedness, and there is at least some evidence for this in our closest living relative, the chimpanzee (Hopkins, Bales, & Bennett, 1993). These findings suggest that handedness has

its origin in nonhuman lateralities, and there is now increasing evidence for consistent lateral preferences not only in primates, but also in rodents and other mammals (see Bradshaw & Rogers, 1993, for a review). Thus, we would join with many others in speculating that human lateral preferences probably arose from lateral biases in nonhuman species, although there are many complicating issues, such as the sometimes-conflicting results of studies involving captive- as opposed to wild-nonhuman-primate populations (see Marchant & McGrew, 1996).

As discussed earlier with respect to some of our own work, the observation that task demands influence the magnitude and direction of manual asymmetries has also been of interest in work with nonhuman primates. Fagot and Vauclair (1991), for example, have made the distinction between low- and high-level tasks and discussed how the magnitude and direction of manual asymmetries are affected by these two types of task. High-level tasks, which require finely tuned motor actions, produce strong biases towards using one hand and so are associated with asymmetries of greater magnitude, although the direction does not appear to be as consistently toward right-hand use as in humans. Low-level tasks, which involve simpler or more familiar or well-practised movements, are associated with more symmetrical distributions of bias in hand use. The asymmetries observed in high-level tasks are thought to arise from hemispheric asymmetries in the control processes needed to perform the high-level task. The hand consistently used to perform the task is contralateral to and controlled by this hemisphere. Although there are population-level asymmetries in hand usage, these vary across species of primates, thus this may suggest underlying species differences in hemispheric asymmetries for controlling the high-level movements. Some clues to this question of differences in underlying hemispheric asymmetries have been sought by comparing species on evidence of other neurostructural (e.g. larger brain areas in one hemisphere) or neurofunctional (e.g. ear or visual-hemifield advantages for particular tasks) measures. A number of studies have shown substantial convergence between manual and hemispheric asymmetries of structure and function. This convergence of different asymmetries provides support for the notion of shared mechanisms and for the possibility of homology between human and nonhuman laterality.

One problem in the study of manual asymmetries in nonhuman primates is that it is difficult to differentiate between asymmetries in preference and performance. Typically, asymmetries in performance are inferred from the magnitude and direction of asymmetries in preference (i.e. the hand the animal chooses to use in performing the task). Some investigators have observed consistency between these two measures, whereas others have not (Fagot & Vauclair, 1991). The ability to make this distinction opens opportunities to compare the details of hand performance, an analysis that may be more revealing about underlying hemispheric asymmetries than one that focuses on patterns of hand preference.

Our own data also suggest that the measurement of lateralisation is a complex issue, and that one must know what to measure and how to measure it. Although we have no final answer, the data we have presented indicate that one must assess a number of different aspects of handedness, and that such variables as throwing hand, eyedness, and most particularly footedness, may ultimately prove to be very critical. Our finding that footedness is an important predictor of language lateralisation (cf Searleman, 1980) provides some support for relations between postural control, an integral part of footedness, and language lateralisation in humans, although the details of the nature of those relations have yet to be specified.

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