Eye-dominance, Writing Hand, and Throwing Hand

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Handedness and eye-dominance are undoubtedly associated statistically, although a previous meta-analysis has found that the precise relationship is difficult to explain, with about 35% of right-handers and 57% of left-handers being left eye dominant. Of particular difficulty to genetic or other models is that the proportions are distributed asymmetrically around 50%. The present study asked whether this complicated pattern of association occurred because, following Peters, it is necessary to divide right-and left-handers into consistent handers (who write and throw with the same hand) and inconsistent handers (who write and throw with opposite hands). In an analysis of 10,635 subjects from questionnaire studies, 28.8% of left-handers and 1.6% of right-handers by writing were inconsistent for throwing. Our results also showed that writing hand and throwing hand both relate independently to eyedness, that throwing hand is somewhat more strongly associated with eyedness, and that the awkward asymmetry around 50% is now removed, 24.2% of consistent right-handers being left eye dominant compared with 72.3% of consistent left-handers, and 55.4% of inconsistent right-handers compared with 47.0% of inconsistent left-handers. We conclude that eyedness is phenotypically secondary to writing and throwing handedness. In our discussion we note that eyedness runs in families, we present new data suggesting that writing hand and throwing hand are co-inherited, and we argue that further data are now required to model properly the associations of writing hand, throwing hand, and eyedness, as well as probably also footedness and language dominance.

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† Philip Bryden died in August 1996.

INTRODUCTION

About one third of the population is left eye dominant, preferring to use the left eye rather than the right eye for monocular tasks such as sighting through a tube (see Porac & Coren, 1976, for a review of other definitions of eye dominance). Eyedness is associated with handedness, which is most conventionally assessed in terms of the hand used for writing, with right-handers being more likely to be right eye dominant and left-handers being more likely to be left eye dominant. However, the precise numerical nature of the relationship is extremely difficult to explain, and in a recent meta-analysis of the literature we found that about 35% of right-handers and about 57% of left-handers were left eye dominant (Bourassa, McManus, & Bryden, 1996). Such a pattern of results is not readily explained by any straightforward theory in which handedness and eyedness are phenotypically associated or are genotypically associated using the genetic model of McManus (1985).

The principal problem of the association of handedness and eyedness is that the proportions (35% and 57%) are themselves asymmetrically distributed to either side of a value of 50%, which can be regarded as the biological baseline for laterality, being the proportion of right and left dominance when pure fluctuating asymmetry is the origin of asymmetries (Palmer & Strobeck, 1986). Genetic models that invoke fluctuating asymmetry as one phenotypic form inevitably predict that asymmetries always tend to be to the same side of 50% (e.g. in the case of handedness and the McManus model, the proportion of left-handedness is always less than 50% for all genotypes, and similarly the proportion of right hemispheric language is always less than 50% for all genotypes). The only clear solution to this problem is if two phenotypes are causally associated in some fashion, so that one laterality induces another laterality to be in the same direction. However if that is the case, then if *laterality*$_1$ is to the right and pushes *laterality*$_2$ to the right to some extent, one should expect that when *laterality*$_1$ is to the left then *laterality*$_2$ should be pushed to the left to the same extent i.e. there should be symmetry around 50%. That is what does *not* seem to occur with handedness and eyedness.

The present paper developed out of the work of Peters (Peters, 1990; Peters & Pang, 1992; Peters & Servos, 1989) which has shown that left-handers, defined in terms of the preferred hand for writing, are not a homogeneous group but instead a substantial number are ''inconsistent'', in particular preferring to throw with their right hand (and in fact also being more skilled at throwing with their right hand). If left-handers are a heterogeneous group then the peculiar association of writing hand with eyedness might become explicable. Although Peters has clearly demonstrated the existence of a subgroup of inconsistent left-handers, no estimates were provided of their frequency in the population because the original studies did not use representative samples. Similarly Peters has not published data asking whether, by analogy, inconsistent *right-handers* might also exist who write with their right hand but prefer to throw with their left hand. The extremely large study of Gilbert and Wysocki (1992) did however present data confirming the existence of inconsistent left-handers. It also suggested that inconsistent right-handers do indeed exist, as was suggested by Grimshaw and Bryden (1994). The present paper will confirm these claims, using a different methodology, and finding similar estimates of the incidence of inconsistent right-and left-handedness to the earlier studies.

That throwing hand might be related to eye dominance was regarded as a theoretical possibility on the basis of a very simple analysis based on two premises. First, the literature on eyedness has previously speculated that movements of the two eyes might be controlled by the mechanism of a ‘‘master’’ and ‘‘slave’’. In order to move the eyes to a particular direction, one eye would be moved actively (the master) and the other (the slave) would be yoked to follow. Walls (1951) provides a charming mechanical analogy in the steering mechanism of some early cars in which the steering wheel was connected directly only to one front wheel which it moved directly, and a connecting rod between the front wheels then moved the other wheel indirectly. If such a mechanism indeed existed for control of the movements of the two eyes then control of one one side would result in movement of both eyes. In a strict sense such a theory is, of course, wrong. As Davson (1990, p. 478) puts it, ‘‘we know that the muscles of both eyes are innervated at the same time in any one movement, and it would be quite incorrect to think of the one eye dragging the other along with it, as this view of ocular dominance would require.’’ That view is enshrined in ‘‘Hering’s Law of Equal Innervation’’, which says that the two eyes always move together when producing either version or vergence movements[1]. However, the rule does not seem to apply strictly[2], and the problems can be seen particularly in mixed vergence and version movements. Carpenter (1988, p. 121) suggests that the contribution of each eye to vergence movements is ‘‘not *exactly* equal’’ (emphasis in original). Pickwell (1972a, b) has developed this position and suggests that Hering’s Law is valid as long as vergence movements are measured not from a point exactly midway between the eyes but with respect to a point corresponding to the ‘‘binoculus’’, the subjective sighting centre of the two eyes, which is normally located closer to the eye that is dominant for sighting (e.g. Barbeito, 1981). From the point of view of the

[1] Even if this is true in a strict sense for the actual movements themselves, in that the eyes always move together, it does seem possible to us that one eye may be dominant in the sense that it shows less random error in its positioning than does the other which is merely trying to copy it. In the steering mechanism described by Walls one could imagine that on a bumpy road, with the steering wheel held as still as possible, the sideways jitter of the wheel connected directly to the steering wheel would necessarily be less than that connected only via the track rod, as the latter has two imperfect connections, each allowing movement, compared with only one in the former case.

[2] Hering’s Law of Equal Innervation has recently been suggested to be wrong, based on the results of the neurophysiological studies of Zhou and King (1998), who found that premotor neurones, which were predicted by Hering’s Law to encode signals related to movements of *both* eyes, actually show activity related to the movement of only one eye *or* the other.

present development, it is sufficient to note the argument that eye movements are generated asymmetrically with respect to the dominant eye.

The second component of the present theory was almost naively simple but implied that if eyedness was related to only one of the two types of handedness (writing/throwing) then it was more likely to be related to throwing than writing. To put it bluntly, in making a saccadic eye movement one is, in a sense, throwing the eye to one side. The eye is of fixed mass and in a fixed orbit so that it can be moved remarkably precisely and predictably by such a ballistic mechanism; but that apart, the mechanism is in principle no different from throwing a ball with a hand. If correct, then eyedness should show a clearer and more straightforward relationship with throwing hand than with writing hand. In passing it might be noted that the frontal eye fields, which are important for the control of voluntary saccades, are located only about 20mm anterior to the sensorimotor cortex for the hand (Paus, 1996).

The present study set out to re-analyse data collected by several investigators, originally for other purposes than the present one, to assess whether eyedness did indeed correlate better with throwing hand than writing hand. If the original speculation were supported then that would also provide an opportunity to ask some questions about the relative incidence of writing and throwing hand dominance and their inter-relationship. Analysis of data from other sources also allowed an overview of the possible genetics of writing and throwing, as well as that of eye-dominance, in order to try to formulate a better understanding of the relationship of eye-dominance to handedness.

METHOD

Several studies had been carried out separately by ICM, CP, MPB, and RB, some published in part and others unpublished, in which large numbers of individuals had been asked about their laterality, typically using inventories in which questions were asked, *inter alia*, about writing hand, throwing hand, and eyedness. The present study combines these data, along with previously unpublished performance data collected by Michael Peters (MP) and provided by him for comparative purposes. Table 1 summarises the important aspects of the methodology in each study. Essentially almost all (except MP1) were similar in using questionnaires distributed to large groups of subjects, in all cases except CP3 it being assumed that they were approximately representative of population proportions. CP3 was weighted to include about equal numbers of right-and left-handers, and MP1 was also weighted towards left-handers; these latter two studies have therefore been omitted from calculations estimating population proportions of the various eye and handedness types. The study of Peters (MP1) was different from the other studies in that although the sample sizes were much smaller, handedness, both writing and throwing, as well as eyedness were assessed by performance measures rather than by questionnaires; it therefore

TABLE 1
Samples and Methods Used in Each of the Data Sets

Study	Study Description	Subjects	Classification of Handedness	Classification of Eyedness
ICM1	Sample ICM1 of McManus (1979, 1985)	Cambridge, UK, undergraduate students studied 1977, previously described in McManus (1985).	5-point scale for ''Write a letter legibly'' or ''Throw a ball to hit a target''; ''Either'' responses excluded (No subjects excluded on writing hand, 13 subjects excluded on throwing hand).	Three items (Eye to look down microscope, telescope, or through keyhole) scored on a 5-point scale (1 = Always left, 3 = Either, 5 = Always right); subjects averaging $\leqslant 3$ scored as left-eyed, > 3 as right-eyed.
MPB1	Sample 1 of Bryden; not previously published.	Waterloo, Canada, undergraduate students studied in 1986.	ditto	ditto
RB1	Sample 1 of Boucher and Bryden; not previously published.	Waterloo, Canada, undergraduate students studied 1996. 58.5%% males; age range 18–24; 100% sample in undergraduate classes.	ditto	ditto
CP1	Sample 1, described in Porac (1996), hand preference data only.	Adults studied in British Columbia between 1986 and 1989. Mean age = 44.6 (SD = 17.1), 51.1% male.	Writing hand assessed on a 5-point scale; ''Either'' responses excluded.	One question on a 3-point scale; ''Either'' responses excluded (130 subjects).
CP2	Sample 2, described in Porac (1993), hand preference data only.	Adults studied in British Columbia between 1986 and 1989. Mean age = 40.7 (SD = 15.9), 37.7% male.	ditto	One question on a 3-point scale; ''Either'' responses excluded (121 subjects).
CP3	Sample 3 of Porac; not previously published.	Adults studied in British Columbia between 1993 and 1995; half under 30 and half over 55. Sample selected to contain approximately equal numbers of right and left handers. 40–60% males in all age categories.	Writing hand assessed on a 5-point scale; ''Either'' responses excluded.	Two questions (Looking into a bottle and a keyhole), each on a 5-point scale; items combined.

TABLE 1
Samples and Methods Used in Each of the Data Sets

Study	*Study Description*	*Subjects*	*Classification of Handedness*	*Classification of Eyedness*
CP4	Sample 4, described in Porac, Coren, & Searleman (1986); hand preference data only.	Sample studied between 1981 and 1982 in British Columbia. 35.2% males; mean age = 19.9 (SD = 4.9).	Drawing hand* assessed on a 3-point scale; ''Either'' responses excluded.	Four questions (Looking into a bottle, keyhole, and telescope, and sighting a rifle), scored left = 1, either = 2, right = 3; mean score < 2 scored as ''left eye'', mean score $\geqslant$ 2 scored as ''right eye''.
CP5	Sample 5, described in Porac & Coren (1981), Chapter 11.	Sample studied between 1976 and 1980 across North America. 63.7% males; mean age = 23.0 (SD = 10.0).	ditto	ditto
CP6	Sample 6, described in Porac & Coren (1981), Chapter 10.	Sample studied between 1976 and 1980 in Canada. 38.9% males; mean age = 20.2 (SD = 4.7).	ditto	ditto
CP7	Sample 7, described in Porac & Coren (1981), Chapter 9.	Sample studied between 1976 and 1980 in Canada. 51.4% males; mean age = 17.1 (SD = 2.1).	ditto	ditto
CP8	Sample 8 of Porac; not previously published.	Sample studied between 1995 and 1996, Victoria BC. 29.6% males; mean age = 23.0 (SD = 7.8).	Writing hand assessed on a 3-point scale; ''Either'' responses excluded.	ditto

CP9o	Sample 9, described in Coren & Porac (1980)	Family study; offspring sample. Sample studied between 1976 and 1979 in British Columbia. 51.6% males.	Drawing hand* assessed on a 3-point scale; ‘‘Either’’ responses excluded.	Three questions (Looking into a bottle, keyhole, and sighting a rifle), scored left = 1, either = 2, right = 3; means core <2 scored as ‘‘left eye’’, mean score ⩾2 scored as ‘‘right eye’’.
CP9p	Sample 9, described in Coren & Porac (1980).	Family study; parental sample. Sample studied between 1976 and 1979 in British Columbia. 49.7% males.	ditto	ditto
MP1	Sample 1 of Peters; not previously published.	Laboratory study of sample selected for increased proportion of left-handers.	Performance measures	Performance measures

* In sample CP8 the subjects were asked about both writing hand and drawing hand, and there was a correlation of 0.90 between the two measures.

provides a partial validation of the questionnaire data reported in the rest of the study.

RESULTS

Table 2 summarises the various studies, showing the numbers of individuals who use their right or their left hand for writing (W_R and W_L), the numbers using their right or their left hand for throwing (T_R and T_L), and the numbers who are right- or left-eyed (E_R and E_L). The overall incidence of left handedness for writing (W_L) in the randomly selected samples is 10.8%, which is significantly higher than the incidence of left-handed throwing of 9.1%, both overall (χ^2= 67.5, 1df, P<.001, McNemar test), and in 11 of the 12 population-based studies (binomial test, P<.001). The overall incidence of left eye dominance is 28.6%. As reported by Peters, there is a substantial number of individuals who are left-handed for writing but are right-handed for throwing; these "inconsistent left-handers" (L_i) represent 28.8% of left-handers. In addition there is a minority of individuals using the right hand for writing who also prefer to throw with the left hand; these "inconsistent right-handers" (R_i) form 1.6% of the right-handers in the studies combined, and as right-handers are more numerous than left-handers, are almost as frequent in the population overall as inconsistent left-handers.

The relationship between writing hand, throwing hand, and eye dominance is shown in the summary statistics at the bottom of Table 2. The incidence of right-eyedness in W_R–T_R, W_L–T_R, W_R–W_L, and W_L–T_L individuals is 24.2% (N= 9557), 55.4% (N= 184), 47.0% (N= 423) and 72.3% (N= 1000) respectively. Several important findings are apparent in these results. First, throwing hand is more strongly associated with eye dominance than is writing hand. Classifying on writing hand, 24.77% of 9741 W_R are E_L compared with 64.8% of 1423 W_L, giving an odds ratio for the association of 5.58 times (95% confidence interval 4.96–6.28); in comparison, classifying on throwing hand, 25.2% of 9980 T_R are E_L, compared with 69.7% of 1184 T_L, giving an odds ratio of 6.83 times (95% confidence interval 5.98–7.79), demonstrating the greater association with throwing hand than writing hand, each estimate being outside the 95% confidence interval of the other. In addition, of the cross-lateral individuals, 55.4% of 184 W_R–T_L are left-eyed, compared with 47.0% of the 423 W_L–T_R individuals who are left-eyed, the difference almost being significant at the P<.05 level (χ^2 = 3.62, 1df, P= .057), and suggesting once again that eye-dominance more strongly follows throwing hand than writing hand.

The data of Table 2 are suitable for hierarchical log-linear modelling. Overall there are large main effects for writing hand, throwing hand, and eyedness (χ^2 = 6985, 7957, and 1872 respectively, 1df, P<.001 in each case); these merely indicate that the marginal proportions are significantly different from 50%, and are of no real interest. Of more theoretical interest is that there are

TABLE 2

Proportions of Right- and Left-handed Throwers and Writers, and Right- and Left-eyed Individuals

Writing hand *Throwing hand* *Dominant eye*	W_R T_R E_R	W_R T_R E_L	W_R T_L E_R	W_R T_L E_L	W_L T_R E_R	W_L T_R E_L	W_L T_L E_R	W_L T_L E_L	$\%W_L$	$\%T_L$	$\%E_L$	$\%R_i$	$\%L_i$
ICM1	533	246	11	5	21	8	35	75	14.9	13.5	35.8	2.0	20.9
MPB1	326	78	2	6	6	3	9	22	8.8	8.6	24.1	1.9	22.5
RB1	189	90	3	0	9	9	4	17	12.1	7.5	36.1	1.1	46.2
CP1	326	99	4	6	8	5	5	21	8.2	7.6	27.6	2.3	33.3
CP2	357	90	7	3	7	4	17	28	10.9	10.7	24.4	2.2	19.6
CP4	435	153	4	4	18	18	11	28	11.2	7.0	30.3	1.3	48.0
CP5	1794	528	26	22	42	38	64	160	11.4	10.2	28.0	2.0	26.3
CP6	850	278	3	3	21	18	25	67	10.4	7.7	28.9	0.5	29.8
CP7	1305	355	6	12	37	29	32	93	10.2	7.7	26.2	1.1	34.6
CP8	112	23	0	1	1	2	6	3	8.1	6.8	19.6	0.7	25.0
CP9p	614	201	5	11	8	2	14	32	6.3	7.0	27.7	1.9	17.9
CP9o	254	102	3	3	7	9	13	36	15.2	12.9	35.1	1.7	24.6
Total	7095	2243	74	76	185	145	235	582	10.8	9.1	28.6	1.6	28.8
CP3	113	59	8	26	20	35	29	100	—	—	—	—	—
MP1	38	9	—	—	19	19	13	41	—	—	—	—	—
Total	7246	2311	82	102	224	199	277	723	—	—	—	—	—
$\%E_R$	24.2% (9557)		55.4% (184)		47.0% (423)		72.3% (1000)		—	—	—	—	—

highly significant interactions between writing and throwing ($\chi^2 = 3956$, 1df, $P < .001$), writing and eyedness ($\chi^2 = 847.2$, 1df, $P < .001$), and throwing and eyedness ($\chi^2 = 157.2$, 1df, $P < .001$), none of which is unexpected. The effect size for writing $\times$ eyedness (log odds ratio = 1.024, SE = .1003, odds ratio = 2.784) is smaller than that for throwing $\times$ eyedness (1.361, SE = .15, odds ratio = 3.900) when both are entered into the model simultaneously. Of particular theoretical importance is that there is no writing $\times$ throwing $\times$ eyedness interaction ($\chi^2 = 2.4$, 1df, NS) indicating that the effects of writing hand and throwing hand on eye-dominance are independent. Differences between the 14 studies were also entered into the analysis. There were large interactions of study $\times$ writing, study $\times$ throwing, study $\times$ writing $\times$ throwing and study $\times$ eyedness ($\chi^2 = 585.1$, 72.0, 89.0, and 72.2 respectively, 13df, all $P < .001$), which primarily indicate differences in selection of subjects between studies. Of more interest is that there are no or only just significant interactions between study $\times$ writing $\times$ eyedness, study $\times$ throwing $\times$ eyedness, and study $\times$ writing $\times$ throwing $\times$ eyedness ($\chi^2 = 16.80$, 12.67, and 22.92 respectively, 13df, NS, NS, and $P = .043$ respectively), indicating no or only minimal differences between studies in the relationship of eyedness to writing and throwing hand.

Figure 1 shows the proportions of individuals in various groups who are left eye dominant. It is apparent in row(a), in which is plotted the percent ($\pm$ 1 SE) of individuals who are left-eyed separately for W_R and W_L subjects, that the

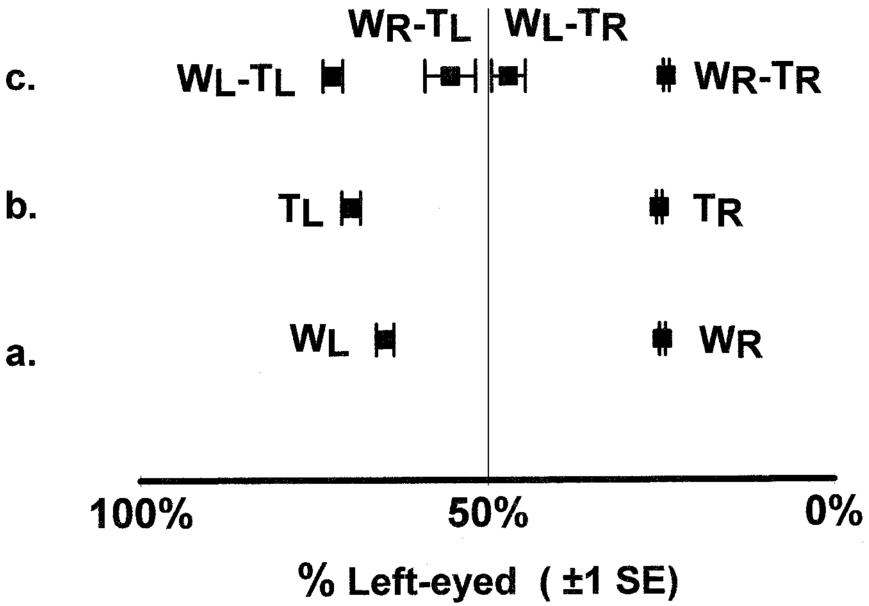

FIG. 1. The proportion of individuals who are left eye dominant, in relation to writing hand, throwing hand, and writing and throwing hand.

proportions are distributed asymmetrically around 50%. Row (b) shows a similar plot for T_R and T_L and although there is clearly a stronger association with throwing hand than there was for writing hand, T_R and T_L are still distributed asymmetrically around 50%. Row (c) shows the proportions of left-eyed individuals in W_R–T_R, W_L–T_R, W_R–T_L, and W_L–T_L subjects. W_R–T_R and W_L–T_L subjects now seem to be symmetrically distributed around 50% as also, within sampling errors, are W_L–T_R and W_R–T_L individuals. The symmetry can be tested more formally by comparing the percentage in one group with (100-percentage) in the other group. The W_R–T_R and W_L–T_L groups do differ significantly in their proportions (24.2% vs 100–72.3% = 27.7%; $\chi^2 = 6.0$, 1df, $P < .01$), perhaps not surprisingly given the huge sample size, although the effect is small when expressed as an odds ratio (1.20; 95% CI = 1.04–1.39). The comparison of W_L–T_R and W_R–T_L groups is not significant (55.4% vs 100–47.0% = 53.0%; $\chi^2 = 0.3$, 1df, NS, odds ratio = 1.10 CI = .78–1.56)).

DISCUSSION

In this study 28.8% of left-handed writers and 1.6% of right-handed writers showed inconsistent handedness, preferring to throw with the hand contralateral to their preferred writing hand. These proportions are compatible with the figures found by Gilbert and Wysocki (1992) in their massive survey of over one million individuals where, considering the 251,881 males and 336,483 females who were in the age range 10–40 (in which the incidences of handedness did not vary with age), 32.4% of male and 37.5% of female left-handed writers threw with their right hand, and 1.55% of male and 1.05% of female right-handed writers threw with their left hand; and with the smaller study of Grimshaw and Bryden (1994), where 35.4% of 322 left-handed writers and 2.25% of 1640 right-handed writers were inconsistent for throwing. We can therefore conclude that crossed writing and throwing hand is a reliable phenomenon in a minority of both left-handers and right-handers.

Our data are also consistent with another finding of the Gilbert and Wysocki study. We found that the overall incidence of left-handed throwing was slightly less than the overall incidence of left-handed writing. In the Gilbert and Wysocki study the appropriate figures (again for the 10–40 age range) are 10.2% of males being left-handed throwers as compared with 13.0% being left-handed writers, and 7.3% of females being left-handed throwers compared with 10.1% being left-handed writers. This result clearly removes one possible explanation of our own finding, which was that a slightly higher number of subjects in some of the studies said they used ‘‘either’’ hand for throwing and were removed from the analysis; in the Gilbert and Wysocki study, subjects classified themselves only as left-or right-handed and therefore all subjects are included in the analysis. However, in interpreting the result it must be remembered that in the Gilbert and Wysocki study it is also the case that in the older subjects the incidence of left-handed writing becomes less than the incidence of left-handed throwing, for reasons that are not entirely clear but which may reflect writing hand as being more subject to social pressures. Finally it should be stated that the overall incidences of handedness and of eyedness are consistent with meta-analyses that we have reported elsewhere (Bourassa et al., 1996; McManus, 1991; Seddon & McManus, 1993), confirming the general validity of the findings.

Making sense of our results presents problems at two very different levels. First there is the problem of explaining how eye-dominance might be related in functional terms to the two separate forms of handedness shown by throwing and writing. Second there is the problem, already encountered in our previous study (Bourassa et al., 1996), of explaining the precise numbers of right-and left-handers who are left-eyed. We presume that the latter problem can best be explained by some form of genetic model, although as yet there are insufficient data to specify it precisely. Nevertheless in this discussion we will provide and review some other data on patterns within families of writing hand, throwing hand, and eyedness which may help illuminate the problem.

The Functional Relationship of Writing Hand, Throwing Hand, and Eye-dominance

Interpreting the functional inter-relationships suggested by the present results is not easy. The clearest feature would seem to be that eye-dominance shows two separate and separable influences, one dependent on throwing hand and the other dependent on writing hand. The precise manner in which these two aspects of handedness are related to eyedness is obscure but one possible model is based on the theory of Milner and Goodale (1995, p. 179) who propose that the visual system is divided into two separate streams ''coding for perception and coding for action'', the perceptual or ''ventral'' stream terminating in the infero-temporal cortex whereas the action or ''dorsal'' stream terminates principally in posterior parietal cortex. It is clear from studies they report, in particular that of Goodale, Pélisson, and Prablanc (1986), that motor action involves a sophisticated co-ordination between movements of the eyes and movements of the hands, and that therefore throwing is likely to be strongly associated with the dorsal stream. In addition they also report evidence that when right-handed subjects make simultaneous eye and hand movements to an object then the latency of eye movements is greater when a left-hand movement is being made than when a right-hand movement is made (Fisk & Goodale, 1985), implying that the functional organisation of eye movements is primarily in the left hemisphere (Goodale, 1988). The association of writing hand with the ventral stream is slightly less compelling, except that writing *par excellence* is concerned with the production of visual forms in a limited spatial domain (often of small extent and restricted to two dimensions, as compared with the production of relatively simple actions in a complex three-dimensional space in throwing).

One of the few clues to the underlying neural basis of eyedness has been the claim of Coren and Porac (1976) that objects in the dominant eye appear larger than those in the non-dominant eye. This might be explicable on the basis that estimation of size, along with other complex object properties involving the integration of information, is primarily a function of infero-temporal cortex. It might be objected that Milner and Goodale's patient DF seemed to be able to process size of objects accurately without a ventral visual system, but that ignores the fact that her responses were readily confounded by stimuli such as a vertical slot composed of thick horizontal lines (Milner & Goodale, 1995, p. 142), or even with a T-shaped slot which would often be rotated through 90 degrees (ibid, p. 138). Why it should be useful for the dominant eye to over estimate the size of an object is not immediately clear but one clue might lie in the mechanisms of binocular perception. As pointed out by Richards (1975), if the eyes converge asymmetrically on an object that is relatively close to the eye, then one image is optically magnified relative to the other. This can be corrected by taking vertical disparities into account as well as horizontal, but it may well leave a residue, particularly if, as a result of eye dominance, asymmetrical convergence is more common to one side than the other.

In speculating on the relationship between the two visual systems and eye-dominance we are aware of two potential problems. First, Milner and Goodale themselves suggest that the dorsal stream is not lateralised (1995, p. 112); that may be correct at the level of the parietal lobes, but is unlikely to be true later on in the action system, as hand control itself is highly asymmetric. Second, although Milner and Goodale imply that the ventral visual system seems almost *too* lateralised for explanatory comfort (to us), with apperceptive agnosias occurring principally after unilateral right hemisphere damage (1995, p. 146), and pure alexia after left hemisphere damage (1995, p. 150), there is a clear discrepancy between hemispheric dominance and eye-dominance, as dominance of an eye is for two hemi-fields, each of which projects to a different cerebral hemisphere. This problem may be superable in terms either of a concomitant naso-temporal asymmetry (see e.g. Beaton, 1979), or, alternatively, if there were evidence that the effects reported by Coren and Porac were actually restricted by hemi-field as well as by eye. The latter possibility is being followed up at present.

The Numerical Inter-relationships between Writing Hand, Throwing Hand, and Eye-dominance

In a previous paper (Bourassa et al., 1996) we were unable to provide any satisfactory explanation for the relationship between handedness and eye-dominance. In particular, it did not seem to be possible to account for the particular numerical proportions found by a model that we called ''phenotypic'', ''genotypic'', or ''pheno-genotypic''. Only the latter managed to provide some prediction of the proportions of right-and left-handers who were left-eyed, and it also made predictions about the inheritance of handedness in families that were clearly falsified. The data presented so far avoid some of those problems. In particular the clear symmetry that is now found between writing hand, throwing hand, and eyedness fits with what we have called a phenotypic model. That is, an individual who is right-handed for throwing and writing is more likely to be right-eyed to the same extent that an individual who is left-handed for throwing and writing is more likely to be left-eyed; and similarly for right writers/left throwers and vice versa. The phenotype of handedness therefore determines the phenotype of eyedness. We have phrased it in this way because the incidence of eyedness is substantially closer to 50% (i.e. fluctuating asymmetry) than is the incidence of writing hand or throwing hand, and hence we presume that handedness is prior to eyedness in causal terms. The incidence of eyedness is presumably closer to 50% than is the incidence of handedness because of random noise in the causal chain, which results in some individuals whom one might expect to be right-eyed becoming left-eyed and vice-versa. Eyedness is likely therefore to be down stream from handedness.

Much more problematic for the current data is to explain the proportions of right-hand and left-handers who are inconsistent, and also to explain the apparent inheritance of eyedness, which would seem to run in families. It should be said at this stage that at present we are not aware of any published studies in which writing hand, throwing hand, and eyedness have all been assessed simultaneously in families. Here therefore we will consider three subsets of the possible data: the association of eyedness in families, the association of eyedness in twins, and the association of writing hand and throwing hand in families. Although not a complete part of the picture they will nevertheless show that eyedness does run in families and that there is a co-inheritance of writing hand and throwing hand. These data will therefore constrain any possible genetic (or for that matter, other) models of the relationship between writing hand, throwing hand, and eyedness.

Eyedness in Families. This need not be reviewed in any detail because Reiss and Reiss (1997) have recently reviewed the published literature, as well as presenting new data of their own. Taking together the eight studies reviewed, there is a clear tendency for the proportion of left-eyed children to increase as the number of left-eyed parents increases, rising from 26% ($n = 966$) when both are right-eyed, through 38% ($n = 788$) when one is left-eyed, to 44% ($n = 209$) when both are left-eyed. Modelling of these by log-linear modelling finds a highly significant interaction of parental eyedness and offspring eyedness ($\chi^2 = 41.3$, 2df, $P < .001$). However more detailed scrutiny of the data suggests that there are substantial differences between some of the studies, and the study $\times$ parental eyedness $\times$ offspring eyedness interaction is also highly significant ($\chi^2 = 46.4$, 14df, $P < .001$) confirming that the differences cannot be explained by differences in marginal proportions or chance variation. The aggregate results alone are suggestive of a similar genetic model to that proposed elsewhere for handedness, principally because in none of the groups does the incidence of left-eyedness exceed 50%. However that is not the case for all of the studies, and in some subgroups there are proportions that are significantly greater than 50%, in particular the L × L group of Reiss. Another problem is that in some of the data sets, in particular those of Annett (1985) and of Strangmann-Koehler and Ludwig (1954) there is little evidence of a familial trend or else it is reversed from that expected. In interpreting these data it should be remembered, as Reiss and Reiss (1997) point out, that the data of Strangman-Koehler and Ludwig are restricted to families containing at least one left-hander. We simply have no explanation of these discrepancies. Nevertheless there does seem to be indisputable evidence for an overall familial trend in eyedness.

Eyedness in Twins. There are four published papers that have reported some data on eyedness in twin pairs, albeit that some are very limited. Unfortunately the study of Wilson and Jones (1932) did not report data on eyedness in pairs (nor on its relationship to writing hand and throwing hand, both of which had been measured). In addition the British National Child Development Study, information about other aspects of which have been reported elsewhere (McManus, 1981; McManus & Mascie-Taylor, 1983), also recorded eyedness in the twin pairs. It has been analysed by one of us (ICM) and data are reported here for the first time: Table 3 summarises the results. Taking the studies together, among the 128 monozygotic twin pairs, 67 (52.3%) are discordant for eyedness, in comparison with an expected proportion of 49.9% under a binomial distribution. For the dizygotic twins, 98/234 (41.9%) were discordant for eyedness compared with a binomial expectation of 48.9%. There is therefore some slight evidence of concordance in the DZ twins but none at all in the MZ twins. In part this may reflect the fact that under genetic models of laterality which include a component of fluctuating asymmetry it is expected that a high proportion even of MZ twins will be discordant, as has been found for handedness (Annett, 1985; McManus, 1980; McManus & Bryden, 1992).

Throwing Hand and Writing Hand in Families. We are unaware of any previously published data that examine the association of writing hand and throwing hand in families. Here we therefore report two sets of data, aspects of which have been previously published. In both studies parents and a single offspring have each completed handedness questionnaires which included questions about both writing hand and throwing hand. In study ICM2 (McManus, 1985) questionnaires were distributed to undergraduate students and their parents at the time of graduation, whereas in the second study (MPB2), undergraduates were asked to take the questionnaires home so that their parents could complete them (Bryden, Singh, & Rogers, 1995). Table 4 summarises data

TABLE 3
Eyedness in Monozygotic and Dizygotic Twins Pairs Based on Published and Unpublished Data

	Monozygotic			Dizygotic		
	R–R	*R–L*	*L–L*	*R–R*	*R–L*	*L–L*
Rife (1933)	4	13	0	—	—	—
Stocks (1933)	4	23	13	15	41	26
Kovác & Ruisel (1974)	—	5	—	—	—	—
Koegler & Koegler (1986)	17	10	7	26	21	20
National Child Development Study (McManus; unpublished)	7	21	9	10	36	39
Total	32	67	29	51	98	85

on the patterns of co-inheritance of writing hand and throwing hand. It can be seen that the numbers in many of the cells are fairly small and therefore a comprehensive analysis is not possible. Instead a simple analysis will be carried out to show that the transmission of writing hand in families is contingent not only on writing hand but also on throwing hand. The various combinations of parental handedness shown in the first column of Table 4 will be reduced to three groups. When both parents are consistent right-handers (i.e. W_R–T_R) then in study ICM2 12.6% of the 382 offspring are W_L, whereas if one or more of the parents is a left-handed writer than 23.9% of the 46 offspring are W_L($\chi^2 = 4.45$, 1df, 1df, $P < .05$). Such proportions are compatible with those summarised elsewhere (McManus & Bryden, 1992). The co-inheritance of writing hand and throwing hand can be shown by studying those parents where both write with their right hand but at least one is an inconsistent right-hander (i.e. W_R–T_L). There are 44 offspring of such individuals of whom 12 (27.3%) are W_L, a proportion that is almost identical to the proportion of offspring when one or more parents is W_L, and which is significantly higher than when both parents are consistent right-handers ($\chi^2 = 7.05$, 1d, NS). It would seem therefore that inconsistent right-handers act as if they are left-handed writers in terms of the number of left-handed offspring that they produce. The MPB2 data show a broadly similar pattern: of the 363 offspring of two consistent right-handers, 10.2% are left-handed, compared with 15.9% of the 63 offspring of parents in which one or more is a left-hander, and 19.4% of the 31 offspring where both are W_R but one or both is an inconsistent right-hander. The trend does not quite achieve conventional statistical significance ($\chi^2 = 2.46$, 1df, $P = .116$ two-tailed, $P = .058$ one-tailed). However when the ICM2 and MPB2 studies are combined the effect is very clearly significant ($\chi^2 = 9.51$, 2df, $P = .009$). These results therefore strongly suggest that there is co-inheritance of writing hand and throwing hand.

TABLE 4
Patterns of Co-inheritance of Writing Hand and Throwing Hand

	Study ICM2 Offspring				Study MPB2 Offspring			
Mother × *Father*	W_R–T_R: R_c	W_R–T_L: R_i	W_L–T_R: L_i	W_L–T_L: L_c	W_R–T_R: R_c	W_R–T_L: R_i	W_L–T_R: L_i	W_L–T_L: L_c
$R_c \times R_c$	323	11	8	40	321	5	15	22
$R_i \times R_c$	12	1	1	5	11	1	1	4
$R_c \times R_i$	18	0	1	5	13	0	1	0
$R_i \times R_i$	1	0	0	0	0	0	0	0
$L_c \times R_c$	17	1	1	5	23	2	1	2
$R_c \times L_c$	9	0	1	2	16	0	0	3
$L_i \times R_c$	1	0	0	1	4	0	0	0
$R_c \times L_i$	5	0	0	1	7	0	0	2
$L_i \times R_i$	1	0	0	0	0	0	0	0
$L_c \times L_i$	1	0	0	0	0	0	0	0
$L_c \times L_c$	0	0	0	0	1	0	0	2
$R_c \times R_c$	323	11	8	40	321	5	15	22
$R_{i/c} \times R_{i/c}$	31	1	2	10	24	1	2	4
L × R / R × L / L × L	34	1	2	9	51	2	1	9

Handedness in parents and offspring in two family studies of handedness, with handedness classified according to writing and throwing hand. R_c (consistent right-handedness: W_R–T_R); L_c (consistent left-handedness: W_L–T_R). $R_{i/c} \times R_{i/c}$ indicates pairs of parents in which both use the right hand for writing, but at least one member of the pair is an inconsistent right-hander.

Writing and Throwing Hand in Twins. We know of only one study that has asked about writing and throwing hand in twins (Gedda et al., 1981), but regrettably we find the results almost impossible to analyse in any meaningful way.

Conclusions

The present study clarifies our understanding of the origin of eye-dominance, suggesting strongly that it is phenotypically secondary to handedness as defined by writing hand and throwing hand. The underlying mechanisms by which writing and throwing exert their influences on eye-dominance are still not clear, but the invocation of two separate cortical visual streams, one dorsal and the other ventral, may provide some theoretical underpinning and point the way to further studies. Alternatively it is possible as handedness may well reflect cerebellar asymmetries (McManus & Cornish, 1997), and eye movement abnormalities are a recurrent feature of cerebellar disease, that handedness and eye-dominance may be linked through the cerebellum. Much more problematic is how to explain the relationship between writing hand and throwing hand. Family patterns of writing hand have previously been explained fairly adequately by a simple genetic model such as that of McManus (1985) or Annett (1985), but neither model has as yet been generalised to explain the co-inheritance of throwing hand and writing hand, not least because there are very few existing data in the literature on which a model can be based. The present analyses provide suggestive evidence that there is indeed co-inheritance, but provide little in the way of strong data for constraining any more formal genetic model. The patterns of family transmission of eye-dominance are at least qualitatively compatible with those of handedness, the overall higher incidences of left eye dominance presumably reflecting some form of noise which means that the overall incidence of left-eyedness is closer to 50% than is the overall incidence of left-handedness. We nevertheless feel fairly confident that any genetic model of writing and throwing hand should fairly straightforwardly be able to explain the patterns of eye-dominance in families and twins. It would seem that if these lines of enquiry are to develop further than a priority must be to obtain adequately sized population samples which look simultaneously at the patterns of inheritance of writing hand, throwing hand, and eyedness in large samples. Other work also suggests that language lateralisation is related not only to writing hand, but also that dichotic listening asymmetry is predicted by an interaction of writing hand, eyedness, and familial sinistrality (Bryden, 1988), and that inconsistent left-handers differ from consistent left-handers in their pattern of dichotic lateralisation (Grimshaw & Bryden, 1994), and there is recent work suggesting that footedness maybe as good or even a better predictor of language lateralisation as handedness (Elias & Bryden, 1998). Taking all these results together suggests that the time is ripe for studies assessing the complete inter-relationships between writing hand, throwing hand, footedness, eyedness, and language lateralisation in a large sample of individuals, preferably in families.

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