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Handedness and Eye-dominance: A Meta-analysis of Their Relationship

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About one in ten people is left-handed and one in three is left-eyed. The extent of the association of handedness and eyedness is unclear, as some eyedness measures are potentially contaminated by measures of handedness.

A meta-analysis of hand–eye concordance in 54,087 subjects from 54 populations, found that concordance was 2.69 × greater in questionnaire rather than performance studies, 1.95 × greater in studies using unimanual monocular performance measures, and 6.29 × greater in studies using non-sighting measures of eye-dominance. In the remaining studies, which seemed to show no evidence of bias, the odds-ratio for hand–eye concordance was 2.53 ×; in a population with 9.25% left-handedness and 36.53% left-eyedness, 34.43% of right-handers and 57.14% of left-handers are left-eyed. This pattern of hand–eye association poses problems for genetic models of cerebral lateralisation, which must invoke pleiotropic alleles at a single locus or epistatic interactions between multiple loci. There was no evidence that the incidence of eyedness, or the association between eyedness and handedness, differed between the sexes.

INTRODUCTION

Most people are right-handed, preferring to use the right hand for skilled and also unskilled activities. Most people are also right-eyed, preferentially using their right eye for sighting tasks, or for carrying out monocular activities such as looking down a microscope or through a telescope. However about 10% of the population prefer to use their left hand and about 30% prefer to use their left eye

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in such situations. The figures imply that at least 20% of the population will prefer to use one hand and the other eye. Many theorists, particularly in the area of education, have focused on this phenomenon. At various times the educational system has strongly encouraged all children to write with the right hand. Although manifest handedness may be altered by training, no attempts are made to change the sighting eye. Many authors (e.g. Delacato, 1959, 1963, 1966; O'Connor, 1965) have thus seen eyedness as a more fundamental measure of an underlying laterality. By these arguments, crossed eye–hand dominance is a danger sign, indicative of a child being trained to use the less biologically suited hand for writing (although we note that Bishop, 1983, examined 16 studies, in only two of which was there marginal evidence of an increased incidence of crossed dominance in children with reading difficulties). The Ortonian view of handedness and eyedness necessarily implies that there is a high positive association between handedness and eyedness. Furthermore it suggests that the association should be greater in cultures or times when there is little pressure to force children to be right-handed.

Despite having been written about for at least 400 years (Porta, 1593), and probably recognised much earlier, surprisingly little is known about eye-dominance, at least in comparison with handedness. In the best review of the phenomenon, Porac and Coren (1976), on the basis of the study of Coren and Kaplan (1973), carefully distinguish sighting dominance (the usual sense of the term eye-dominance, as described earlier) from sensory dominance (concerned with binocular rivalry) and acuity dominance (concerned with differences between the eyes in visual acuity), with both of which sighting dominance is uncorrelated. A wide range of performance measures of sighting dominance has been proposed (Porac & Coren, 1976), Walls (1951) describing some 25 different measures. Some techniques are very simple, involving the mere holding up of a finger or a paper or metal cone, whereas others use complex pieces of optometric equipment. A concern about many of these forms of assessment is that the measure of lateralisation of eyedness is contaminated by handedness; thus for instance observing the eye used to sight down a rifle may produce a spurious association with handedness due to the rifle typically being held with a finger of the dominant hand on the trigger; similarly if a subject is asked to look through a small object such as a telescope or kaleidoscope which is held in one hand, then the holding of the object in the dominant hand may well distort measures of the association between handedness and eyedness. Additionally eyedness has sometimes been assessed using questionnaires concerned with monocular activities (Coren & Porac, 1978; Crovitz & Zener, 1962; Hull, 1936). These show two specific problems; first the items may refer to activities such as holding a rifle, which are contaminated by hand preference (Coren, 1993); and second there may be a process of set, whereby once a subject has consistently answered "right" (or "left") to many handedness items, then they will merely carry on answering "right" (or "left") to other questions concerning eye preference. One purpose of the present meta-analysis is to assess the extent to which the association between handedness and eyedness has been distorted by what we will refer to as *measurement bias*; it should be distinguished from *selection bias* in which there is a non-population incidence of left-handedness or left-eyedness, for whatever reason.

If the concept of eyedness is to be a useful one, then it should be reliable. It is therefore worth noting that a number of studies (Cuff, 1931; Miles, 1929; Piran, Bigler, & Cohen, 1982; Updegraff, 1932) have found high consistency of repeated measures of sighting dominance, typical reliability coefficients being 0.94 (Piran et al., 1982) and 0.97 (Cuff, 1931), with other studies reporting a ‘‘high’’ degree of reliability (Miles, 1929, 1930; Updegraff, 1932), but without sufficient data to allow calculation of a precise reliability coefficient.

Relatively little is known about the functional origins of eyedness, although probably many researchers would agree with the position of Peters (1991) that just as a bilateral brain is likely to have problems in co-ordinating the rapid movements of the larynx and vocal apparatus in producing speech, so bilateral control will also be ineffective in eye movements, where ‘‘the medial rectus of one eye has to be coordinated with the lateral rectus muscle of the other eye’’ (p. 310), so that the process may be better controlled by a single, unilateral control mechanism.

Despite little being known about the functional purpose of eyedness, or about its neural origins, there have nevertheless been a large number of studies that have assessed eyedness, very often in association with handedness. Many of these studies were carried out by educationalists, child psychologists, and paediatricians dealing with children with developmental learning problems, typically dyslexia. Much of this work has drawn its theoretical inspiration from the influential studies of Orton (1925, 1937), who claimed that many such disorders arose as a result of ‘‘crossed-laterality’’, in which the child was either right-eyed and left-handed or left-eyed and right-handed. Subsequently, Delacato (1959, 1963, 1966) has suggested that consistent handedness and eyedness (and footedness) is necessary for normal intellectual development, particularly of reading and speech. Despite the fact that large-scale surveys have shown no association between crossed laterality and intellectual abilities (McManus & Mascie-Taylor, 1983), such theories continue to be influential.

Hand preference has been known and written about since ancient times, and there is presently a consensus that it runs in families (Brackenridge, 1982; McManus & Bryden, 1992), and is probably, although not certainly, genetic in origin. Handedness is also associated, albeit imperfectly, with cerebral lateralisation of language, an association that current genetic models of handedness can readily explain by means of pleiotropy of the single gene at the single locus. Left-handedness is accounted for in both models by the existence of a ‘‘chance’’ gene—C (McManus, 1985) or RS- (Annett, 1985)—in which handedness is determined partly as a result of fluctuating asymmetry

(McManus & Bryden, 1992); it is this chance allele that is responsible for the low level of concordance of handedness in monozygotic twins. The lack of convincing evidence of population-level asymmetries of handedness or pawedness in non-human species, (Ward & Hopkins, 1993; and also see commentaries on MacNeilage, Studdert-Kennedy, & Lindblom, 1987), coupled with the inability to breed animals in which right- or left-pawedness runs in families (Collins, 1969), suggests that in non-humans the only gene present in the gene-pool is the C or RS- allele.

A number of studies have also found evidence for eyedness running in families (Brackenridge, 1982; Coren & Porac, 1980; Merrell, 1957; Zoccolotti, 1978), although not all have done so (Annett, 1985). Brackenridge (1982) has reported that the proportion of left-eyed offspring is 27% in R × R matings, 36% in R × L matings, and 45% in L × L matings. Although not identical to the results concerning handedness in families, the data do suggest that a broadly similar genetic model may be responsible, in which fluctuating asymmetry plays a moderate part. Such a type of model would also be supported by the low concordance of eyedness in monozygotic twins; Kovác and Ruisel (1974), in the only published study of eyedness in twins of which we are aware, reported that 5 out of 11 MZ pairs were discordant for eyedness.

The extent of the association of handedness and eyedness has important implications for the nature of genetic theories of handedness and eyedness. If there is no proper association of handedness and eyedness, then genetic models must propose the existence of two independent genetic systems—in the same way as the zero association of handedness and *situs inversus* must mean that two independent genetic systems are involved (Cockayne, 1938; McManus, 1991; Torgersen, 1950; Woods, 1986). However if there is an association between handedness and eyedness then it must result either from pleiotropy of a single genetic system, or epistatic interactions between two or more genetic systems. The size of the hand–eye association, and its particular form, therefore have implications for genetic models of both handedness and eyedness, and for the understanding of cerebral lateralisation in general.

In this study we therefore report a meta-analysis of studies of the hand–eye association, we assess the extent to which this association is modified by possible artifacts of measurement, we assess the most likely form of the association of handedness and eyedness in those studies without measurement bias, and we consider the implications of the hand–eye association for possible genetic models.

METHOD

A computerised literature search was carried out in October 1992, using PsycLIT and Medline, for papers indexed as referring to eye-dominance, eyedness, or ocular dominance. These papers were examined for all studies that reported the relationship between handedness and eye dominance. Additionally all papers cited by these studies were also followed up, as were further citations by those papers, etc. A total of 47 papers contained data that were usable for the meta-analysis, in that the data could be cast into a 2 × 2 table relating eye dominance to handedness. In some papers data were reported from two or more geographically separate areas, or using two or more distinct methodologies; in such cases the data were regarded as coming from separate studies (and are reported as such in Table 1), resulting in 54 sets of data being analysed.

In a number of papers, data were reported that could not be used; examples include studies in which handedness was not classified in a usable fashion, typically because handedness (and/or eyedness) was scored as a continuous variable only (Porac & Coren, 1975a, 1979b; Porac, Coren, & Duncan, 1980b; Piran et al., 1982; Previc & Saucedo, 1992), or because handedness was measured in an unusual fashion (Adams, 1965; Brown, Tolsma, & Kamen, 1983). Additionally we excluded studies in which handedness was divided into three groups; right, left, and mixed, and in which mixed-handers were more frequent than left-handers (e.g. Clark, 1957; Brito, Paumgartten, & Lins, 1989; Groden, 1969; Gureje, 1988; Kovác & Benuskova, 1975; Rymar et al., 1984; Smith, 1933); in cases where mixed handedness was less frequent than left handedness, mixed and left-handers were combined. In some studies eyedness was assessed as acuity dominance rather than sighting dominance (Geldard & Crockett, 1930; Woo, 1930; Woo & Pearson, 1927); alternatively, eyedness was classified on a 3-point scale (Coons & Mathias, 1928; Hoosain, 1990).

In some studies insufficient data were given to reconstruct the 2 × 2 table relating handedness to eye dominance (Channon, 1985; Coren & Kaplan, 1973; Cornell, 1938; Cuff, 1931; Friedlander, 1971; Groden, 1969; Gronwall & Simpson, 1971; Helveston, Billips, & Weber, 1970; Miles, 1928; Ong & Rodman, 1972), or the reporting of the study was too confused (Hughes, 1953). In some studies although the 2 × 2 table itself was not reported, it could be calculated from the information given (e.g. Combs, 1983). Additionally some studies were omitted because they duplicated data already published elsewhere in a different form (e.g. Gur, 1977; Nachson & Denno, 1986; Porac, Coren, & Duncan, 1980a; Updegraff, 1932); in such cases our table generally reports the study that was earlier or more complete. We only considered individuals from normal and not pathological populations (thereby excluding some studies, e.g. Marlow, Roberts, & Cooke, 1989; Swiercinsky, 1977); however where possible we did use normal controls from studies that assessed clinical or pathological populations.

TABLE 1

Details of the Studies Used in the Meta-analysis

Study	*Subjects*	*Investigators*	*Handedness Assessment*	*Eyedness Assessment*	*Mean/ estimated mean age (range)*	*Number of subjects*	*LH-LE/LH-RE/RH-LE/RH-RE*	*%LE*	*%LH*	*Association (Odds-ratio)*
Mills, 1925	American ophthalmic patients	Other	Questionnaire	E.1.d	N/K	1000	93/17/130/760	22.30	11.00	31.14✕
Downey, 1927*	American college students, high school and public school students	Psychologist	Questionnaire	E.1.b	37 (8–65)	1233 ♂716 ♀517	140/91/305/697 ♂74/57/158/427 ♀66/34/147/270	(36.09) (♂32.40) (♀41.20)	(18.73) (♂18.30) (♀19.34)	3.51✕ ♂3.49✕ ♀3.53✕
Miles, 1930	American university, high school, and grade school students, professors, and visiting Chinese university students.	Psychologist	Questionnaire	E.1.a.ii	22 (14–50)	187	16/14/43/114	31.55	16.04	3.00✕
Quinan, 1931	American university students, and traffic offenders	Other	Performance	E.1.b	25 (18–30)	2694	102/97/597/1898	25.95	7.39	3.34✕
Jasper, 1932*	American adolescents and university students	Psychologist	Questionnaire	E.1.a.ii	20 (12–38)	149	17/14/38/80	(36.91)	(20.81)	2.52✕
Lund, 1932	American junior and senior high school students, and college students	Psychologist	Performance	E.1.a.ii	20 (15–24)	234	10/2/52/170	26.50	5.13	13.64✕
Eyre & Schmeeckle, 1933	American junior high school students	Psychologists	Performance	E.1.a.ii	15 (11–18)	193	7/2/15/169	11.40	4.66	32.81✕
Updegraff, 1933	American preschool children	Psychologist	Performance	E.1.a.ii	4 (2–6)	59	4/2/15/38	32.20	10.17	4.47
Gates & Bond, 1936	American children/ controls in study of retarded readers	Educationalists	Performance	E.1.c	5 (5–6)	68	2/3/24/39	38.24	7.35	1.15✕
Witty & Kopel, 1936	American children/ controls in reading disability study	Educationalists	Questionnaire	E.1.c	10 (7–12)	64	3/4/18/39	32.81	10.94	1.66✕

Fink, 1938	American optometry clinic patients	Other	Performance	E.1.d	N/K	125	4/3/29/89	26.40	5.60	3.90×
Castner, 1939	American children at child development clinic	Psychologist	Performance	E.1.a.ii	10 (4–15)	72	2/1/20/49	30.56	4.17	4.02×
Schonell, 1941	English children, controls in study of reading disability	Educationalist	Performance	E.1.a.ii	10 (5–15)	69	3/2/19/45	31.88	7.25	3.27×
Lavery, 1944	Irish children and adults, random sample	Other	Questionnaire	E.1.d	31 (8–54)	389	27/0/101/261	32.90	6.94	141.70×
Hildreth, 1945	American elementary school children	Psychologist	Performance	E.1.a.ii	9 (6–11)	177	9/11/59/98	38.42	11.30	1.37×
Stevenson & Robinson, 1953	American kindergarten children	Educationalists	Performance	E.1.d	5 (5–5)	68	5/2/23/38	41.18	10.29	3.60×
Merrell, 1957	Unspecified	Other	Performance	E.1.c	22 (18–25)	497	20/13/137/327	31.59	6.64	3.62×
Meuhl, 1963	American pre-school children from university co-operative	Educationalist	Performance	E.1.a.ii	5 (4–5)	62	6/8/14/34	32.26	22.58	1.82×
Harmon, 1966*	American ophthalmic clinic patients	Other	Performance	E.1.d	N/K	100	8/5/31/56	(39.00)	(13.00)	2.77×
Rengstorff, 1967	American optometry patients, army officers, cadets, and army recruits	Other	Questionnaire	E.1.a.ii	24 (5–75)	5479	241/211/1587/3440	33.36	8.25	2.47×
Stephens, Cunningham & Stigler, 1967*	American elementary school children age	Educationalists	Performance	E.1.c	6 (6–6)	89 ♂44 ♀45	19/10/27/33 ♂11/6/11/16 ♀8/4/16/17	(51.68) (♂50.00) (♀53.33)	(32.58) (♂38.64) (♀26.67)	2.26× ♂2.54× ♀2.00×
	Temne (Sierra Leone) adults	Psychologist	Performance	E.1.a.ii	27 (20–35)	121 ♂106 ♀15	2/2/33/84 ♂2/2/27/75 ♀0/0/6/9	28.93 ♂27.36 ♀40.00	3.31 ♂3.77 ♀0.00	2.52× ♂2.75× ♀1.46×
Dawson, 1972	Australian aboriginal adults	Psychologist	Performance	E.1.a.ii	27 (20–35)	95 ♂56 ♀39	8/2/29/56 ♂4/2/19/31 ♂4/0/10/25	38.95 ♂41.07 ♀35.90	10.53 ♂10.71 ♀10.26	6.51× ♂2.91× ♀21.86×
Gur & Gur, 1974*	American university students	Psychologists	Questionnaire	E.1.b	22 (18–25)	87 ♂47 ♀40	13/15/17/42 ♂9/9/4/25 ♀4/6/13/17	(34.48) (♂27.66) (♀42.50)	(32.18) (♂38.30) (♀25.00)	2.12× ♂5.67× ♀0.90×
Chaurasia & Mathur, 1976	Indian medical students and teachers	Others	Questionnaire	E.1.b	25 (17–36)	313 ♂237 ♀76	10/20/97/186 ♂8/14/69/146 ♀2/6/28/40	34.19 ♂32.49 ♂39.47	9.58 ♂9.28 ♀10.53	0.98× ♂1.24× ♀0.55×

Study	Subjects	Investigators	Handedness Assessment	Eyedness Assessment	Mean/ estimated mean age (range)	Number of subjects	LH-LE/LH-RE/RH-LE/RH-RE	%LE	%LH	Association (Odds-ratio)
Hardyck, Petrinovich & Goldman, 1976	American children at community schools	Psychologists	Performance	E.1.a.ii	9 (6–11)	7686	429/311/2528/4418	38.47	9.63	2.41 ×
Dawson, 1977	American and Alaskan Eskimo children and adults	Psychologist	Performance	E.1.a.ii	17 (13–20)	80	10/10/12/48	27.50	25.00	3.88 ×
Gur & Gur, 1977	American adult hospital workers and non-psychiatric hospital patients	Psychologists	Questionnaire	E.1.c	35 (18–55)	200 ♂100 ♀100	11/11/56/122 ♂10/6/27/57 ♀1/5/29/65	33.50 ♂37.00 ♀30.00	11.00 ♂16.00 ♀6.00	2.17 × ♂3.38 × ♀0.61 ×
Van-Camp & Bixby, 1977	American children from three school districts	Psychologists	Performance	E.1.c	7 (5–8)	311	18/20/118/155	43.70	12.22	1.18 ×
Birkett, 1979*	British volunteers from schools, colleges and general public	Psychologist	Questionnaire	E.1.b	23 (16–42)	125 ♂54 ♂71	38/14/39/34 ♂11/10/16/17 ♀27/4/23/17	(61.60) (♂50.00) (♀70.42)	(41.60) (♂38.89) (♀43.66)	2.32 × ♂1.62 × ♀4.55 ×
Hovsepian, Slaymaker, & Johnson, 1980	American undergraduates	Psychologists	Questionnaire	E.1.a.i	22 (18–25)	74	19/6/16/33	47.30	33.78	6.09 ×
Porac, Coren, & Duncan, 1980a	Canadian preschool and high school students from community day care centres and community high schools	Psychologists	Performance	E.1.a.ii	10 (3–19)	555	19/12/172/352	34.41	5.59	3.19 ×
Porac & Coren, 1981	North Americans ''from a broad range of socioeconomic categories''	Psychologists	Questionnaire	E.2.a	21 (8–99)	5147 ♂2756 ♀2391	411/198/1075/3463 ♂247/125/500/1884 ♀164/73/575/1579	28.87 ♂27.10 ♀30.91	11.83 ♂13.50 ♀9.91	6.68 × ♂7.43 × ♀6.14 ×
Hebben, Benjamins, & Milberg, 1981	American elementary school children	Psychologists	Questionnaire	E.1.c	8 (5–11)	191 ♂104 ♀97	9/8/51/123 ♂4/5/22/73 ♀5/3/29/60	31.41 ♂25.00 ♀35.05	8.90 ♂8.65 ♀8.25	2.68 × ♂2.67 × ♀3.22 ×
Noonan & Axelrod, 1981*	American university students	Psychologists	Performance	E.1.c	22 (18–25)	192	26/34/42/90	(35.41)	(31.25)	1.64 ×

Van-Camp, 1981	American elderly adults from a retirement community, and two senior centres	Psychologists	Questionnaire	E.1.a.ii	75 (62–98)	114 ♂21 ♀93	4/2/43/65 ♂1/1/8/11 ♀3/1/35/54	41.23 ♂42.86 ♀40.86	5.26 ♂9.52 ♀4.30	2.71× ♂1.35× ♀3.58×
Combs (1983)*	143 US College students	Psychologist	Questionnaire	E.1.b	29 (18–40)	143	18/19/31/75	(34.26)	(25.87)	2.27×
Rymar, Kameyama, Niwa, Hiramatsu, & Saitoh, 1983	Japanese school children	Other	Performance	E.1.c	10 (3–15)	853	31/8/271/543	35.40	4.57	7.42×
	Japanese adults; controls in study of schizophrenia	Other	Questionnaire	E.1.b	29 (15–99)	565	11/21/180/353	33.81	5.66	1.05×
Nachson, Denno, & Aurand, 1983	White American children in Philadelphia Collaborative Perinatal Project (CPP)	Psychologists	Performance	E.1.a.ii	7 (6–7)	514 ♂259 ♀255	37/27/190/260 ♂22/16/90/131 ♀15/11/100/129	44.16 ♂43.24 ♀45.10	12.45 ♂14.67 ♀10.20	1.86× ♂1.98× ♀1.74×
	Black American children in Philadelphia Collaborative Perinatal Project (CPP)	Psychologists	Performance	E.1.a.ii	7 (6–7)	6732 ♂3326 ♀3406	467/300/2501/3464 ♂242/156/1203/1725 ♀225/144/1298/1739	44.09 ♂43.45 ♀44.72	11.39 ♂11.97 ♀10.83	2.15× ♂2.22× ♀2.09×
Shan-Ming, Flor-Henry, Dayi, Tiangi, Shuguang, Zenxiang, 1985*	Random sample of Chinese adults	Psychologists	Performance	E.1.a.ii	30 (16–73)	432 ♂200 ♀232	16/15/68/333 ♂7/10/24/159 ♀9/5/44/174	19.44 ♂15.50 ♀22.84	7.18 ♂8.50 ♀6.03	5.18× ♂4.65× ♀6.77×
Hoogmaartens & Caubergh, 1987	Belgian youths and adults	Others	Questionnaire	E.2.a	23 (15–32)	128	10/2/32/84	32.81	9.38	10.92×
Whittington & Richards, 1987	British National Child Development Study (NCDS)	Other	Performance	E.1.a.i	11 (11–11)	10513	563/320/2703/6927	31.07	8.40	4.51×
Costeff, Reshef, Bergman, Koren, Solzi, Greenbaum, Itzkowitz, 1988	Israeli children (sibling controls of hemiplegic children), and ‘‘healthy adults’’	Other	Performance	E.1.a.ii	42 (3–81)	57	5/1/14/37	33.33	10.53	9.48×
Brown & Taylor, 1988	British naval ratings	Psychologists	Performance	E.1.a.i	23 (16–43)	186	19/6/29/132	25.81	13.44	13.47×
Bryden, 1988*	Canadian adults, mostly undergraduate students	Psychologist	Questionnaire	E.1.a.ii	22 (18–25)	297	46/32/48/171	(31.64)	(26.26)	5.06×
Bryden, 1989*	Canadian introductory psychology students	Psychologist	Questionnaire	E.1.b	20 (18–25)	686 ♂358 ♀328	89/70/143/384 ♂43/44/78/193 ♀46/26/65/191	(33.81) (♂33.80) (♀33.84)	(23.17) (♂24.30) (♀21.95)	3.40× ♂2.40× ♀5.13×

Study	Subjects	Investigators	Handedness Assessment	Eyedness Assessment	Mean/ estimated mean age (range)	Number of subjects	LH-LE/LH-RE/RH-LE/RH-RE	%LE	%LH	Association (Odds-ratio)
Levander, Schalling, & Levander, 1989*	Swedish university students	Psychologists	Questionnaire	E.1.c	22 (18–25)	162	25/53/16/68	(25.30)	(48.14)	1.98 ×
						♂76	♂12/25/4/35	(♂21.05)	(♂48.68)	♂3.87 ×
						♀86	♀13/28/12/33	(♀29.07)	(♀47.67)	♀1.27 ×
Dargent-Paré, de Agostini, Mesbah, & Dellatolas, 1992	French adults, mainly students and employees	Psychologists	Questionnaire	E.2.a	25 (15–35)	2088	141/54/374/1519	24.66	9.34	10.53 ×
						♂940	♂61/21/150/708	♂22.45	♂8.72	♂13.47 ×
						♀1148	♀80/33/224/811	♀26.48	♀9.84	♀8.69 ×
	Greek adults, mainly students and employees	Psychologists	Questionnaire	E.2.a	22 (15–35)	634	23/17/89/505	17.67	6.31	7.58 ×
						♂352	♂11/11/50/280	♂17.33	♂6.25	♂5.55 ×
						♀282	♀12/6/39/225	♀18.09	♀6.38	♀10.98 ×
	Italian adults, mainly students and employees	Psychologists	Questionnaire	E.2.a	30 (15–35)	613	32/13/128/440	26.1	7.34	8.25 ×
						♂435	♂24/12/92/307	♂26.67	♂8.28	♂6.52 ×
						♀178	♀8/1/36/133	♀24.72	♀5.06	♀20.73 ×
	Algerian adults, mainly students and employees	Psychologists	Questionnaire	E.2.a	25 (15–35)	571	20/12/163/376	32.05	5.60	3.78 ×
						♂281	♂11/2/70/198	♂28.83	♂4.63	♂12.95 ×
						♀290	♀9/10/93/178	♀35.17	♀6.55	♀1.73 ×
	Spanish adults, mainly students and employees	Psychologists	Questionnaire	E.2.a	25 (15–35)	614	30/8/129/447	25.90	6.19	12.40 ×
						♂317	♂18/7/56/236	♂23.34	♂7.89	♂10.33 ×
						♀297	♀12/1/73/211	♀28.62	♀4.38	♀23.98 ×

Studies marked with an asterisk, and for which incidences of left-eyedness and left-handedness are in parentheses, are those in which there is evidence that the selection of subjects was not random with respect to handedness and eyedness.

Measures

A range of measures was obtained from each study:

Handedness. Studies were divided into those in which handedness was measured by a questionnaire or inventory {H1} and those in which handedness was measured by performance of tasks {H2}.

Eyedness. Studies were divided into several sub-groups on the basis of how eyedness was assessed. These are summarised in Table 2, and principally divide studies into those that used performance versus questionnaire measures, those in which monocular or binocular measures were used, and those in which there was potential for contamination from handedness. The classification was constructed *a priori* and in the event none of the studies met criterion E2.b, and therefore E2 overall was compared with the categories of E1.

For statistical analysis the degrees of freedom in the six eyedness groups were partitioned into five non-orthogonal contrasts: *EC1:* Performance *vs.* Questionnaire measures {E1.a.i, E1.a.ii, E.1.b, E1.c, E1.d *vs.* E2}; *EC2:* Monocular performance measures *vs.* all others {E1.a.i, E1.a.ii *vs.* E1.b, E1.c, E1.d, E2}; *EC3:* Unimanual monocular performance measures *vs.* all others {E1.a.i *vs.* E1.a.ii, E1.b, E1.c, E1.d, E2}; *EC4:* Mixed performance measures *vs.* all others {E1.c *vs.* E1.a.i, E1.a.ii, E.1.b, E1.d, E2}; and *EC5:* ''Other'' measures of dominance *vs.* all others {E1.d *vs.* E1.a.i, E1.a.ii, E1.b, E1.c, E2}.

Ethnic Group. The studies were broadly divided into White and non-White groups. Within the White group, studies were sub-divided into those principally of Northern European extraction and those of Southern European extraction. The non-White group was also sub-divided into Oriental (China and Japan) and others. Four non-orthogonal contrasts were used to explore differences between the four groups: *EG1:* Caucasian *vs.* All others; *EG2:* Southern Europeans *vs.* All others; *EG3:* Non-Caucasian, Non-Oriental *vs.* All others; and *EG4:* Oriental *vs.* All others.

Investigators. The investigators in a study were divided into three groups: ''Psychologists'', ''Educationalists'', and ''Others'' (principally medical or ophthalmic). Group was determined either from the known professional affiliation of authors, or the journal of publication. The three degrees of freedom were partitioned into two non-orthogonal contrasts: I1: Educationalists and Psychologists *vs.* Others; and I2: Educationalists *vs.* All others.

Age of Subjects. The mean age of subjects in each study was estimated as accurately as possible from the information provided in the studies. Sometimes the range of ages was wide and/or the information provided was limited.

TABLE 2

Summary of the Classification of the Methods of Measuring Eye Dominance

{E1}: Eyedness assessed by performance of a task. These were sub-divided into:	{E1.a}: Eyedness assessed by a monocular procedure, in which sighting was primarily with a single eye chosen by the subject. These were further subdivided into:	{E1.a.i}: The sighting object or instrument (e.g. telescope, tube of paper, gun, etc.), was held in one hand or to one side, thereby making contamination with handedness possible.
		{E1.a.ii}: The sighting object or instrument, typically the large cone or tube used in a manoptoscope, was held bimanually.
	{E1.b}: Eyedness assessed by a binocular procedure in which both eyes are observing a target or object, and either the subject or the experimenter then observes which eye is aligned with the target	
	{E1.c}: Eyedness assessed by a combination of methods E1.a.i, E1.a.ii, and E1.b	
	{E1.d}: Eyedness assessed, either partially or completely, by some other method of assessment, typically those in which the eyes are observed for phoria during rivalrous viewing by the two eyes.	
{E2}: Eyedness assessed by means of a questionnaire. *A priori* these were further subdivided into two groups:	{E2.a}: Questionnaire items included tasks that were unimanual (e.g. firing a rifle), and therefore potentially biased (e.g. the questionnaire of Coren & Porac, 1978).	
	{E2.b}: Questionnaire items are all unbiased by exclusion of asymmetric items involving the use of the dominant hand.	

Year of Data Collection. If the date of data collection was specified then that was used, otherwise the year of publication was used, less four years (estimated as a typical time between data collection and eventual publication).

Statistical Analysis

In all of the studies analysed the data could be reduced to a 2 × 2 contingency table showing the relationship between handedness (classified as right or left) and eyedness (also classified as right or left). The association between handedness and eyedness was calculated for the *i*th study as an odds-ratio, γ_i, adjusted for continuity for the small number of cases in which cells with zero entries were found.

$$\gamma_i = \frac{(N_{L,L_i} + 0.5).(N_{R,R_i} + 0.5)}{(N_{L,R_i} + 0.5).(N_{R,L_i} + 0.5)}$$

Statistical analysis was in terms of $\log_e(\gamma_i)$, because its confidence interval is symmetric as compared with the asymmetric confidence interval of γ_i, and it generally has more desirable mathematical properties.

Studies varied in size (range = 57–10513; mean = 1042; SD = 2112; median = 192) and therefore estimates of γ were weighted in the statistical analysis to take account of these large differences. The method of weighting is essentially similar to that described by Hedges for other effect size estimators (Hedges, 1982). For the *i*th study, e_i, the inverse of the sampling variance of $log_e(\gamma_i)$, s_i is calculated as:

$$e_i = \frac{1}{s_i} = \frac{1}{\frac{1}{N_{L,L_i}} + \frac{1}{N_{L,R_i}} + \frac{1}{N_{R,L_i}} + \frac{1}{N_{R,R_i}}}$$

From the values of e_i, the weight for a particular study, w_i, is calculated as:

$$w_i = \frac{n.e_i}{\sum_{i=1,n} e_i}$$

where n is the number of studies. This method has the advantage of weighting estimates of γ_i in proportion to their sampling error, and yet also keeping the total degrees of freedom in the analysis the same as the number of studies (thereby following the recommendations of Hunter & Schmidt, 1990, who emphasise that the appropriate sample size in a meta-analysis is the number of *studies* and not the number of *subjects*), and it is effectively the same sort of weighting recommended by Hedges (1982). Statistical analysis of effect sizes used a multiple regression approach (Hedges & Olkin, 1983), which allowed for predictors to be continuous and non-orthogonal. Calculation of heterogeneity χ^2 statistics followed the method described by Hedges (1982).

In the multiple regression analyses, in which stepwise entry methods were used, Bonferroni corrections were used to take account of inflation of significance levels due to repeated testing. Essentially, if N variables were entered into the analysis, then the nominal alpha level was set to 0.05/N to achieve a studywise alpha level of 0.05.

RESULTS

Data were analysed from a total of 54,087 subjects in 54 populations from 47 studies for whom there was information on the association of handedness and eyedness. In 11 of the studies there was evidence that subjects had been specifically selected as being of a particular eyedness or handedness. These studies with *selection bias*, which are indicated in Table 1 by parentheses around the values of the incidence of left-handedness and left-eyedness, were therefore omitted from the meta-analyses of the overall incidence of eyedness or handedness, leaving a sub-total of 50,824 subjects from 43 populations. It should be noted that selection bias, the non-random selection of subjects by handedness or eyedness, does not affect the estimate of the hand–eye association using an odds-ratio, and therefore all data were included for that part of the analysis.

Table 1 summarises data from the studies in the analysis. Table 3 shows descriptive statistics for the measures of the incidence of handedness and eyedness (in the studies without selection bias), and for their association (in all studies), in relation to the method of measurement of eyedness, the type of investigator, and the ethnic origin of the subjects.

The Incidence of Eyedness

Taken across all of the studies that showed no evidence of selection bias in the selection of subjects, 33.24% of subjects were left-eyed. A multiple regression was carried out in which the incidence of left-eyedness was the dependent variable, and the 15 predictors were mean age, year of data collection, the log of the study sample size, the method of measurement of handedness, and dummy variables corresponding to the method of measurement of eyedness, the type of investigator, and the ethnic origin of the subjects. Weighting was by means of the total sample size, scaled such that the total degrees of freedom in the regression analysis was the same as the total number of studies being analysed. Analysis was by means of a forward entry, stepwise regression, with a studywise significance level of $P = 0.05$, corresponding to a nominal significance level of $0.05/15 = 0.0033$. None of the variables achieved significance at the 0.0033 significance level.

TABLE 3

Summary of Weighted Mean Incidence of Right-eyedness, Left-handedness and the Odds-ratio for Eye-hand Association by Method of Eyedness Assessment, Type of Investigator, and Ethnic Origin of Subjects.

	Studies without selection bias *and hence suitable for assessing the incidence of eyedness and handedness*				*All studies*					
Group	*N studies*	*N subjects*	*% Left-eyed*	*% Left-handed*	*N studies*	*N subjects*	*Mean* $log_e(\gamma)$	*Geometric Mean* γ	*Heterogeneity* χ^2	χ^2 *per study*
Methods of eyedness assessment										
{E1.a.i}: Performance: Monocular asymmetric	3	10773	31.09	8.66	3	10773	1.534	4.64×	5.04	1.68
{E1.a.ii}: Performance: Monocular symmetric	19	22918	38.01	9.73	21	23364	0.900	2.46×	38.93**	1.85
{E1.b}: Performance: Binocular	3	3572	27.92	7.31	8	5846	1.070	2.91×	19.07*	2.38
{E1.c}: Performance: Mixed	7	2184	35.22	7.37	10	2627	0.826	2.28×	16.38	1.64
{E1.d}: Performance: Other	4	1582	26.05	9.55	5	1682	2.766	15.88×	23.94***	4.79
{E2}: Questionnaire	7	9795	27.13	9.91	7	9795	2.005	7.43×	10.92	1.56
Investigator										
Psychologist	25	27880	35.08	10.18	35	30954	1.208	3.35×	229.03***	6.54
Educationalist	5	331	35.35	11.48	6	420	0.755	2.13×	1.36	0.23
Other (principally medical)	12	22613	30.93	8.09	13	22713	1.336	3.80×	118.23***	9.09
Ethnic origin										
White: Northern European	30	39144	31.97	9.23	41	42407	1.316	3.73×	265.32***	6.47
White: Southern European	4	1918	23.47	6.73	4	1918	2.189	8.92×	0.99	0.25
Non-White: Oriental	6	1850	31.19	5.51	3	1850	1.209	3.350×	7.28	2.43
Non-White: Other	3	7912	42.37	10.91	6	7912	0.786	2.19×	9.49	1.58

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

The Incidence of Handedness

Overall in the studies without evidence of selection bias, 9.26% of subjects were left-handed, a value compatible with that found elsewhere by Seddon and McManus (1993; see also McManus, 1991). Analysis of the variation in incidence of handedness was essentially identical to that for the incidence of eyedness, except for the change in the dependent variable. Only one variable was a significant predictor of the incidence of left-handedness: I1. ''Other'' investigators produced a lower incidence of left-handedness than did psychologists and educationalists combined ($P<0.001$; $b=-2.18$).

The Association between Handedness and Eyedness

Across all studies the mean value of $log_e(\gamma_i)$ was 1.49, equivalent to an odds-ratio of 4.437× (i.e. a left-hander is 4.437× more likely to be left-eyed than is a right-hander). The standard error of the mean value of $log_e(\gamma_i)$ is 0.0591 (using the method of Hedges, 1982), giving a 95% confidence interval for the overall odds-ratio of 4.183× –4.706×. Testing for the homogeneity of effect size revealed a highly significant difference between studies ($\chi^2=355.78$, 54 df, $P<<0.001$).

In order to explore differences between studies, the size of the association between handedness and eyedness, calculated as $log_e(\gamma_i)$, was used as the dependent variable in a stepwise multiple regression. Independent variables were as in the analyses of the incidences of handedness and eyedness; weighting was as described earlier using the values w_i. Four variables were significant predictors, at the 0.0033 level, of the extent of association in a study, the first three of which were contrasts derived from the method of measurement of eyedness; EC1, which contrasted performance measures with questionnaire methods ($P<0.001$, $b=0.989$), studies using questionnaires finding an association 2.69× greater than performance measures; EC5, which contrasted the ''other'' measures of eyedness with the rest ($P<0.001$; $b=1.839$), ''other'' measures of eyedness having an association of 6.29× higher than the remainder of the studies; and EC3, which contrasted unimanual monocular methods with all others ($P<0.001$; $b=0.667$), these methods producing an association 1.95× higher than all other methods combined. The fourth, and least significant, predictor of the odds-ratio, was the average age of the subjects ($P<0.001$; $b=0.0134$/year), older subjects having a greater hand–eye association than younger subjects (1.4× per decade).

In interpreting the result of age it should be remembered that the older subjects were more often assessed using questionnaire methods, and therefore it is possible that the apparent main effect of age may reflect an interaction between age and study method, with only studies with *measurement bias* actually showing an age effect. The analysis was therefore repeated but restricted only to the studies that used methods without measurement bias. The effect of age was then the only significant predictor, but with nominal $P = 0.0424$, which after Bonferroni correction was not significant. We therefore conclude that the association of handedness and eyedness does not change with age. Figure 1 shows the distribution of hand–eye association as a function of age and of measurement bias; it is clear that the biased studies show a higher overall hand–eye association, that they tend to show a linear trend with age, that the unbiased studies show little evidence of a trend with age, and that in particular the exclusion of the one outlying study with a mean age over 70 would not affect that conclusion.

Examination of the 39 studies that used methods E1.a.ii, E1.b, or E1.c— which are symmetric in the sense that both hands are used equivalently during

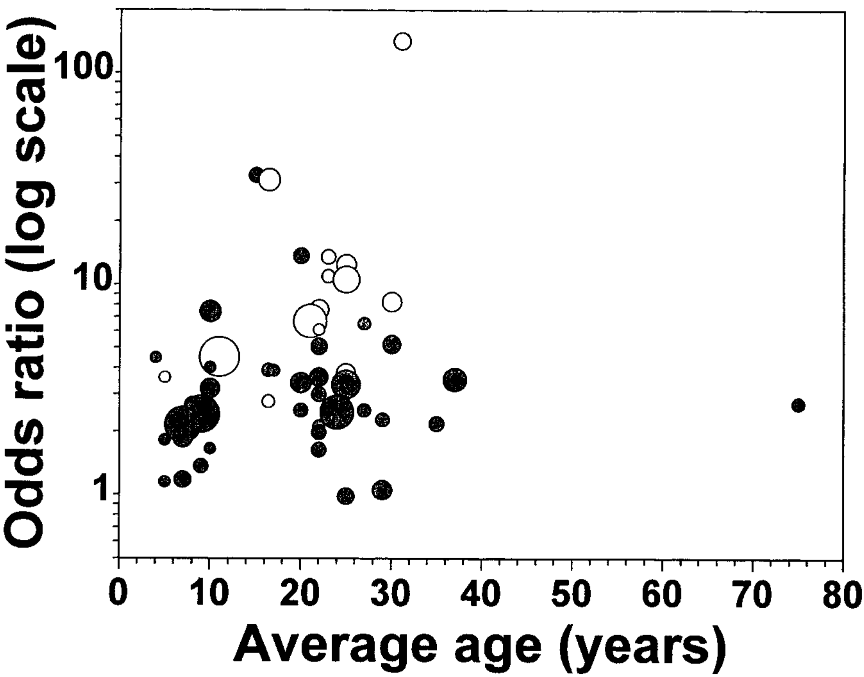

FIG. 1. The relationship of the hand–eye association (plotted as the odds-ratio, γ_i on a logarithmic scale) in relation to the mean age of the subjects in each study, separately for studies without measurement bias (dark symbols) and those studies with measurement bias (open symbols). The diameter of the individual symbols is proportional to the square-root of the sample size, and hence to the standard error of the estimates of the odds-ratio, the more accurate estimates being plotted with larger symbols.

the process of measurement, and therefore are less likely to show measurement bias—showed that the heterogeneity statistic was now substantially reduced in size ($\chi^2 = 78.35$, 39 df, $P < 0.001$). Although this statistic is still highly significant, the warning comments of Hedges (1982) must be borne in mind, concerning very large sample sizes, when it is more important to consider the actual variation in the effect sizes rather than mere significance, as small differences can still result in large chi-square values. In this case we note that for the set of relatively unbiased measurement methods (E1.a.ii, E.1.b, E.1.c) the mean chi-square per study is 78.35/39 = 2.01, compared with a value of 5.30 for the other studies ($\chi^2 = 79.47$, 15 df), and of 6.59 for the entire set of studies ($\chi^2 = 355.78$, 55 df). It is therefore apparent that the majority of variance in effect size is between the methods with and without measurement bias, and between the different types of methods with measurement bias. This can be seen in Table 3, in which the heterogeneity statistics are shown for each of the methods. It now becomes apparent that the different forms of measurement are all of similar homogeneity, with the exception of the ''Other'' methods, which are of necessity heterogeneous in type, and that the mean chi-square per study of the unbiased methods taken together is of the same order of magnitude as the variation within any of the individual methods. A ''funnel plot'' (Fig. 2) of the odds-ratio, $\log_e(\gamma_i)$, in relation to the sample size (on a logarithmic scale), suggests that the biased methods may have a wider spread at all sample sizes, and that the biased methods have a higher overall odds-ratio. Additionally it should be noted that the symmetry of the funnel plot implies an absence of selection bias in the studies examined (Egger & Davey Smith, 1995). Intriguingly there is some apparent loss of expected sampling variability at very small sample sizes, and this may be explained by small studies not being published if they either have negative odds-ratio (i.e. a reverse of the normal association) or very high odds-ratios (i.e. such a high correlation between handedness and eyedness that there are few individuals with crossed dominance).

An Estimate of the Association of Handedness and Eyedness for Unbiased Methods of Measurement

The multiple regression analysis suggested that studies using questionnaires (E2), using unimanual methods of assessment of eyedness (E1.a.i), or using ''other'' methods of assessing eyedness other than conventional sighting dominance (E1.d), showed higher associations of handedness and eyedness. To assess the unbiased association of handedness and eyedness we therefore found the weighted mean value of $log_e(\gamma_i)$ across the 39 studies that did not use methods E1.a.i, E1.d, or E2. This gave a value of the weighted mean of $log_e(\gamma_i)$ of 0.9299 with a standard error = 0.0337 (i.e. $\gamma = 2.53\times$, meaning that left-handers are 2.53× more likely to be left-eyed than are right-handers), with a

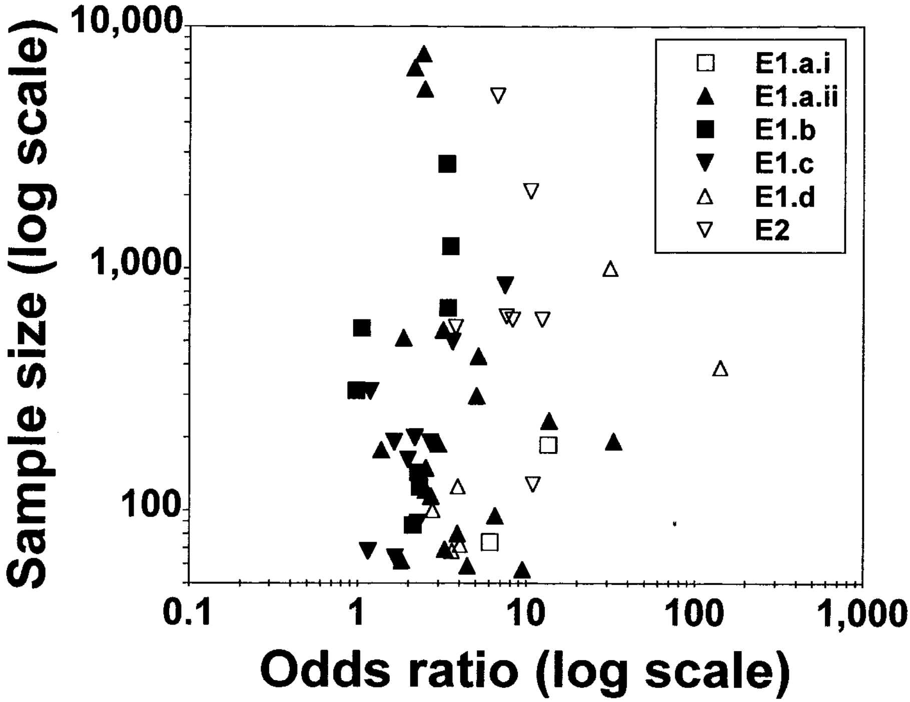

FIG. 2. The "funnel plot" of $\log_e(\gamma_i)$ (the odds-ratio) in relation to sample size (on a logarithmic scale), plotted separately for the different methods of eyedness assessment. The three methods without measurement bias are shown, as in Fig. 1, as solid symbols, and the methods with measurement bias as open symbols.

95% confidence interval of 2.37× –2.71×. As the confidence interval does not include unity, we may conclude that even in the studies that seem to be unbiased, there is nevertheless a significant association between handedness and eyedness. The incidences of right- and left-handedness and right- and left-eyedness in an unbiased population were then calculated from the 29 studies that not only used unbiased measures of eyedness (as mentioned earlier), but also had not shown sampling bias in the selection of subjects based on eyedness or handedness. The mean incidences across all appropriate studies (weighted by sample size) were 9.25% left-handedness and 36.53% left-eyedness. From these values and from the estimated odds-ratio in the unbiased studies mentioned previously it can be calculated that in an unbiased population, 34.43% of right-handers will be left-eyed, compared with 57.10% of left-handers. It is these proportions that must be explained by any genetic or other model of the joint origins of handedness and eyedness.

Sex Differences in Eyedness, Handedness, and the Relationship Between Eyedness and Handedness

There were separate sets of data for male and female subjects in 21 of the studies, with a total of 20,761 individuals—10,775 males and 9986 females.

There were 15 studies in which there was no selection bias on the basis of eyedness or handedness (i.e. there was no specific attempt to increase the numbers of left-handed or left-eyed subjects). The incidence of left-eyedness was 1.153× higher in *females* than males (95% CI: 0.705–1.886×) Males: 32.47% of 9480; females: 35.60% of 8899), a difference that is not statistically different from unity. A similar result was found for the subset of nine studies that also employed unbiased measures of eyedness (Odds-ratio = 1.144×; 95% CI = 0.624–2.102×; Males: 40.67% of 4399; Females: 41.51% of 4313). The incidence of left-handedness was 1.314× higher in *males* than females (95% CI: 0.606–2.847×; Males 11.20% of 9480; Females: 9.53% of 8899) in the set of 15 studies, a difference that is not statistically significant; similar values are found for the subset of nine studies with unbiased measures of eyedness and handedness (1.442×; 95%CI = 0.644–3.141×; Males: 11.64% of 4399; Females: 10.39% of 4313). The numerical values are equivalent to those found in a larger meta-analysis of sex differences in handedness by Seddon and McManus (1993; see also McManus, 1991). Analysis of variation in the log odds-ratio of relative difference in incidence of left-eyedness in males and females and of left-handedness in males and females by a weighted, forward-entry multiple regression using the predictor variables described previously, found that in no cases were any of the predictor variables significant at the 0.05 level.

The difference in the hand–eye association in males and females was calculated as $log_e(\gamma_{i\text{-}males}) - log_e(\gamma_{i\text{-}females})$. The mean weighted value across all the studies was –0.0324, with a standard error of 0.1077, and 95% confidence interval of (–0.243, 0.178), corresponding to the association between females being 0.968× greater than in males (95% confidence interval 0.784× –1.195×). As the odds-ratio is not significantly different from unity, the difference in association between males and females is therefore not significant. A similar result was found for the studies with unbiased assessment of eyedness (odds-ratio = 0.953×, 95% CI = 0.771–1.178×). Stepwise, forward entry, weighted multiple regression using $log_e(\gamma_{i\text{-}males}) - log_e(\gamma_{i\text{-}females})$ as the dependent variable found that none of the predictor variables described earlier was statistically significant. The difference in the hand–eye association of males and females was not therefore related to any of the background variables we had assessed. A similar result was found when the analysis was restricted to those studies in which the measurement of eyedness was carried out by methods regarded as unbiased.

DISCUSSION

This meta-analysis of the association of handedness and sighting-eye dominance has found a number of important results. As we had suspected prior to carrying out the study, the different methods of assessing eye dominance result in different associations between handedness and eye-dominance. In the end, we have isolated 39 studies in which the method of measurement of eyedness was not biased. These studies indicate that the overall incidence of left-eyedness in left-handers is 2.53 × than in right-handers. In the other studies, biases in the measurement of eyedness or handedness lead to an even greater association between the two variables. This increased association is best interpreted in terms of biases resulting from carryover from the measurement of handedness to the measurement of eyedness. When subjects are assessed by methods in which they have to sight through a tube or other object which can be held in one hand, then there is an increased tendency for the dominant hand to pick up the object and place it to the ipsilateral eye; and similarly when questionnaires first ask about handedness and then go on to ask about eyedness it is likely that the repeated ''right'' (or ''left'') answers concerning handedness items then carry over in some subjects to answering ''right'' (or ''left'') on the eyedness items. Finally the much increased hand–eye association of methods using phoria or other optometric processes probably result in an increased association due to the examiner knowing the subject's handedness and either consciously or unconsciously taking that into account when assessing eye dominance. It is of interest that in most of the different methods of measurement the degree of heterogeneity of the studies is relatively small, suggesting that it should be possible, say, when assessing results from a questionnaire study to correct the observed association by a factor derived from the data in Table 3; thus the association found in a questionnaire study is likely to be about 7.43/2.53 = 2.93 times greater than in a performance study using an unbiased measure. Nevertheless such an approach is not optimal; ideally on the basis of these analyses we would recommend that, where possible, eye dominance be assessed by unbiased methods, which are likely to be performance assessments, rather than questionnaires.

Two effects that we did not find are also worth noting. First we found no convincing evidence for sex differences in either the incidence of left-eyedness or the association between eyedness and handedness. Furthermore, the small (non-significant) difference in incidence indicated that there are, if anything, somewhat more left-eyed women than men whereas there are (significantly) more left-handed men than women (Seddon & McManus, 1993); eyedness is therefore similar to hand-clasping and arm-folding in its lack of sex differences (McManus & Mascie-Taylor, 1979). One implication is that any genetic model of handedness that explains the sex differences in handedness (Annett, 1985; McManus & Bryden, 1992) will need to be modified in order to explain the genetics of eye-dominance. A further point is that we found no significant effect of age or year of study on the incidence of eyedness, or its association with handedness. Again this contrasts with the handedness literature, where the proportion of left-handers apparently decreases with increasing age (Cohen & Halpern, 1991; Gilbert & Wysocki, 1992).

The extent of the association of handedness and eyedness can be compared with the association of handedness and other measures. We found an overall odds-ratio of 2.53 in our unbiased studies. If one assumes that about 5% of right-handers and 35% of left-handers show right language dominance, then that results in an odds-ratio of 10.23—substantially higher than the hand–eye association. However taking typical values across studies (see Tables 17, 18, and 19 in McManus, 1985) the association of handedness with language dominance assessed by dichotic listening is about 2.62, assessed by unilateral ECT is about 4.34, and by unilateral intra-carotid sodium amytal is about 7.5. The association of handedness and eyedness is therefore relatively smaller than that of language and handedness, although only by a factor of two to three.

In attempting to explain the association between handedness and eyedness it is necessary to account for the fact that they are neither intimately linked, nor completely unassociated. In trying to explain the nature of the association we will consider in turn four distinct models; the *no association model*; the *phenotypic association model*; the *genotypic association model*; and the *phenotypic–genotypic association model.* The crucial result which requires explanation by any adequate model is the proportion of left-eyedness in right- and left-handers, with 34.43% of right-handers and 57.14% of left-handers being left-eyed.

The No Association Model

Despite it being clear that some methods of assessment of eyedness show clear contamination and crossover between handedness and eyedness (questionnaires, or unimanual sighting tasks, or methods using phoria or other optometric procedures) an important conclusion is that it is clearly the case in studies *not* using these methods that there is still a clear association between handedness and eye dominance. Eyedness is therefore not like behavioural lateralities such as arm-folding and hand-clasping (McManus & Mascie-Taylor, 1979) or structural asymmetries such as *situs* (Cockayne, 1938; Torgersen, 1950), which show no association with handedness, and whose origin must therefore be seen as causally distinct from the origin of handedness (and quite probably due to independent genes). As right-handers are more likely to be right-eyed and left-handers to be left-eyed then they must share some aetiological process.

The Phenotype Association Model

A possible explanation of the hand–eye association could be that eyedness is directly caused by handedness. If this process were perfect then 0% of right-handers and 100% of left-handers would be left-eyed. If the process were imperfect, perhaps due to developmental noise, or measurement error, then if x% of right-handers were left-eyed it would be expected that 100–x% of left-handers would be left-eyed. That is clearly not the case in the data we have found, as it would be predicted that 65.57% of left-handers would be left-eyed, a far higher proportion than the 57.14% actually found. Eyedness cannot therefore be seen as being directly secondary to phenotypic handedness.

An alternative model of phenotypic association, is that eyedness relates not to handedness but to cerebral lateralisation for language. If we assume that about 5% of right-handers and about 30% of left-handers show right-sided language dominance, then if eyedness were always contralateral to language dominance, we would expect 5% of right-handers and 30% of left-handers to be left-eyed. Even if the association is imperfect it must always be the case that as most left-handers are *left* language dominant then a clear majority of left-handers should also be *right* eye dominant, which is clearly not the case. Therefore eyedness cannot be secondary to language dominance.

The Genotype Association Model

In both the McManus (1985) and Annett (1985) genetic models of handedness, language dominance results from a pleiotropic effect of the same gene as determines handedness. Might it therefore be the case that the gene also has a third effect, making the majority of the population right-eyed, and the genotypic association resulting in a secondary association between handedness and eyedness phenotypes? Such a model also fails in that, as with the previous explanation where eyedness is secondary to the language dominance phenotype, the genetic model also predicts that if the majority of right-handers are right-eyed, then a majority of left-handers should also be right-eyed, albeit a lesser majority than is the case with right-handers. The model therefore fails for the same reason. Essentially any genetic model in which individuals either have a prototypical combination of lateralities (i.e. right-handed, right-eyed, and left-language) or show a chance distribution of those characteristics, will always suffer from the problem that a majority of right-handers *and left-handers* will show each of the prototypical phenotypes (right-handedness, right-eyedness, left-language dominance).

The Genotypic–Phenotypic Association Model

A modified form of the McManus genetic model can predict the pattern of association found between handedness and eyedness. In this model the dependence of the eyedness phenotype on the handedness phenotype is itself contingent on the genotype of the individual. Consider a situation in which if there is a probability p that an individual will be left-handed then there is also a probability $p.k + (1–p)(1–k)$ that they will be left-eyed. For DD, for whom $p = 1$, then all individuals will be right-handed of whom k will be left-eyed. For CC individuals, for whom there is a 50% chance of being left-handed, then $0.5k + 0.5(1-k) = 0.5$ individuals will be left-eyed; and for heterozygotes, DC, in whom $p = 0.75$, then $0.75k + 0.25(1-k) = 0.25k$ will be left-eyed. Applying these calculations to the data on eyedness, and with $k = 0.682$, then 34.41% of right-handers and 57.42% of left-handers will be left-eyed, a close approximation to the values actually observed. Although such a model has some attractive features, in particular that it does at least produce plausible estimates of the association between handedness and eyedness, it is seriously lacking at another level. The conclusion of four of the five studies of eyedness in families (Brackenridge, 1982; Coren & Porac, 1980; Merrell, 1957; Zoccolotti, 1978) is that there are moderately strong associations present, with two right-eyed parents typically having of the order of 30% left-eyed offspring, compared with about 50% or so of the children of two left-eyed offspring being left-eyed. The genetic model referred to earlier, which successfully predicts the population hand–eye association, also can predict the proportion of left-eyed individuals by parental eyedness combinations. The values so predicted (RE × RE: 35.8% LE; RE × LE: 36.8% LE; LE × LE 37.7% LE) are clearly massively discrepant with the majority of empirical studies. We therefore are forced to conclude that the simple genotypic–phenotypic association model must also be wrong.

Other Models.

Although the models we have described so far are some of the simplest, they clearly cannot represent the totality of models, as none of them explains the data adequately. Other models do however present difficulties. It is possible that there are two independent genes, one for handedness and one for eyedness and that these are in linkage disequilibrium (Yeo, personal communication). Although possible, we do not find this model convincing, principally because in general linkage disequilibrium is inherently unstable, depending on the low probability of closely linked genes separating during crossing over. Given a large amount of (evolutionary) time then such disequilibrium tends to disappear unless there are other factors maintaining it. Likewise although we concede that other types of genetic model may explain some of the phenomena of handedness and lateralisation in general—e.g. the fluctuating asymmetry model of Yeo and Gangestad (1993)—we cannot see precisely how this would explain the specific pattern of association that we have found.

Conclusions

Although we have not been able to develop a strong model to fit the pattern of data we have observed, we nevertheless feel that our analysis has clarified a number of important issues relating to the measurement of eye dominance and its relationship to handedness. In particular there is a vast mass of studies that are in agreement about the nature of association. We believe that eye dominance is a surprisingly neglected aspect of human lateralisation. Apart from the signal exception of the wide-ranging work of Coren and Porac looking at the physiological and perceptual correlates of eyedness (see e.g. Coren & Porac, 1976, 1977; Porac & Coren, 1975b, 1977, 1978, 1979a, 1982, 1986a, b; Porac, Whitford, & Coren, 1976), there have been few serious attempts to ask *what* eyedness is and *why* it occurs. It is readily observed in most individuals; it presumably has some important relationship to visual processing and visuo-manual co-ordination, although that has yet to be adequately explained; it seems to run in families; it is associated with handedness which is itself associated with language dominance; and it seems unlikely to be subject to cultural pressures and therefore secular trends. All these reasons make it an important topic for future research in laterality, and we believe it may well become an important model system for future research.

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