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Sexual orientation and the size of the anterior commissure in the human brain

(homosexuality/sex difference/sexual differentiation)

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ABSTRACT **The anterior commissure, a fiber tract that is larger in its midsagittal area in women than in men, was examined in 90 postmortem brains from homosexual men, heterosexual men, and heterosexual women. The midsagittal plane of the anterior commissure in homosexual men was 18% larger than in heterosexual women and 34% larger than in heterosexual men. This anatomical difference, which correlates with gender and sexual orientation, may, in part, underlie differences in cognitive function and cerebral lateralization among homosexual men, heterosexual men, and heterosexual women. Moreover, this finding of a difference in a structure not known to be related to reproductive functions supports the hypothesis that factors operating early in development differentiate sexually dimorphic structures and functions of the brain, including the anterior commissure and sexual orientation, in a global fashion.**

A fundamental question of human behavior is the relative contribution of genetic, fetal or neonatal hormonal, and postnatal environmental factors to the etiology of sexual orientation. In laboratory animals, considerable attention has focused on observations that levels of gonadal hormones during a critical period of development determine the sexual differentiation of the brain in terms of many sexually dimorphic functions and structures (1). In contrast, little is known regarding sexual differentiation of the human brain. In terms of function, humans exhibit sex differences in reproductive behavior, gonadotropin secretion (2–4), childhood play behavior (5), and cognitive abilities and cerebral lateralization (6–8). In regions of the brain presumably involved in reproductive function, there are reports of sex differences in the suprachiasmatic nucleus (9), the interstitial nuclei of the anterior hypothalamus 1–3 (10, 11), and the bed nucleus of the stria terminalis (12). In regions of the brain not directly related to reproductive function sex differences occur in cerebral asymmetry (13), in the shape of the corpus callosum (CC) (14, 15), and in the midsagittal area of the massa intermedia and anterior commissure (AC) (16).

Several sexually dimorphic functions and structures reportedly differ in homosexual people. Studies indicate that homosexual men exhibit a luteinizing hormone surge that is intermediate between heterosexual men and women (2, 3), although others have failed to confirm this (4). Morphological differences have been identified in homosexual men in nuclei of the brain that are in regions that influence reproductive physiology and behavior: the volume of the suprachiasmatic nucleus may be larger than in heterosexual men and women (17); and the interstitial nucleus of the anterior hypothalamus 3, which we found to be larger in men than in women (11), is smaller in homosexual men than heterosexual men (18). Homosexual males also exhibit differences in characteristics not directly related to reproductive function: there is an increase in the frequency of left-handedness (19–21), childhood play behavior more often resembles that of girls (22), and scores on tests of visuospatial and verbal abilities (23–26) as well as cerebral lateralization (27) resemble those of heterosexual women more than those of heterosexual men. However, others using different criteria have not found a correlation between sexual orientation and handedness (28) or cognitive abilities (29). We hypothesized that in humans, as in laboratory animals, there is a correlation in the direction of sexual differentiation within a given individual between sexually dimorphic functional characteristics, including sexual orientation, and structural sex differences in the brain that we have identified (11, 12, 16). We now report that a sexually dimorphic structure *not* directly related to reproductive function, the AC, in homosexual men more closely resembles that of heterosexual women than that of heterosexual men in terms of area at the midsagittal plane.

Tissue from presumed homosexual women was not examined in this study because AIDS, which was present in most of the homosexual male subjects, has not specifically affected homosexual women. Therefore, sexual orientation is generally not noted in hospital medical records of women. In contrast, sexual orientation is generally specified in medical autopsy records of all men with AIDS or other diseases that can be either sexually transmitted or result from immunodeficiency.

METHODS

The brains used in this study, which were obtained from three Southern California hospitals between 1983 and 1991, had been removed within 24 hr postmortem and placed directly into acetate-buffered 10% formalin. The present investigators collected 256 samples of brain tissue containing the midsagittal region of the AC from brains that appeared unaffected by neuropathology during routine autopsy. Subsequent to histological analysis of brain samples, medical records were examined for results from histoneuropathology, neurological disorders, cause of death, age, gender, and sexual orientation. Subjects were eliminated from this study when medical records indicated histoneuropathology or disorder(s) potentially influencing the AC (e.g., demyelinating disease; n = 59), bisexual orientation (n = 1), or AIDS when all risk factors for the disease were denied by the patient (n = 3). Male and female subjects were classified as heterosexual when medical records did not indicate homosexual orientation. This procedure generated 34 homosexual men, 84 heterosexual women, and 75 heterosexual men. Before the evaluation of AC area and from the identification codes that included age, sex, and sexual orientation, the subjects were age-matched as closely as possible to obtain 30 triplets—each including a homosexual man, heterosexual man, and hetero-

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Abbreviations: AC, anterior commissure; CC, corpus callosum.

sexual woman (unmatched subjects were not further evaluated).

Without knowledge of gender or sexual orientation, the blocks of tissue containing the AC were cut by hand at the midsagittal plane, and this surface was placed against a glass adjacent to a ruler at the same plane, photographed, and made into slides. These images were projected onto white paper and traced twice at different times. The area of each outline was determined by using a Bioquant Hipad digitizer adjusted to correct for magnification (Bioquant IBM program version 2.1; R & M Biometrics, Nashville, TN), and the two measurements of each AC were averaged. In an attempt to verify that individuals who died of AIDS did not have neuropathology known to increase gross neural structure—namely, edema and vacuolization, seven ACs from homosexual males who died of AIDS and seven ACs from heterosexual subjects who did not die of AIDS were randomly selected, sectioned at 60 μm, stained with thionin, and examined under a light microscope by a neuropathologist.

One-way analyses of variance (ANOVA) were performed between the three groups for age, area of AC, brain weight, area of AC divided by brain weight, postmortem period before autopsy, and period between autopsy and photography. To ascertain that our results were not from the two largest ACs of homosexual males, ANOVA were performed excluding these two samples. Similarly, ANOVA were used to compare homosexual men with AIDS, homosexual men without AIDS, heterosexual men with AIDS, and heterosexual men without AIDS. Post hoc comparisons with the Bonferroni t procedure were used to determine differences between the individual groups. Due to the large range of variation in the size of the AC, Mann–Whitney comparisons of AC area between the three groups were made. Pearson's correlation coefficient was used in all subjects and in the three groups individually to test for correlations between the two tracings and between the following parameters: the area of the AC, age, brain weight, postmortem period before autopsy, and period between autopsy and photography. In an attempt to replicate the original observation of a sex difference in the AC (16), a one-tailed independent t test compared age-matched heterosexual men and women.

RESULTS AND DISCUSSION

There was a highly significant correlation between the measurements of the two tracings ($r = 0.94$, $P < 0.0001$) with no more than a 5% difference between the two tracings of a given subject. The subjects ranged in age from 22 to 59; ages did not differ between groups (ANOVA, $P = 0.45$) (Table 1, Fig. 1). There was a significant difference in the area of the AC between the three groups (ANOVA, $P = 0.0001$): the AC of homosexual men was 18.0% or 2.17 mm^2 larger than that of heterosexual women (Bonferroni t procedure, $P < 0.018$; Mann–Whitney test, $P < 0.0075$) and 34.0% or 3.6 mm^2 greater than that of heterosexual men (Bonferroni t procedure and Mann–Whitney test, $P < 0.0001$). The AC in females was 13.4% or 1.4 mm^2 larger than that of heterosexual men (Bonferroni t procedure and Mann–Whitney test, $P > 0.05$).

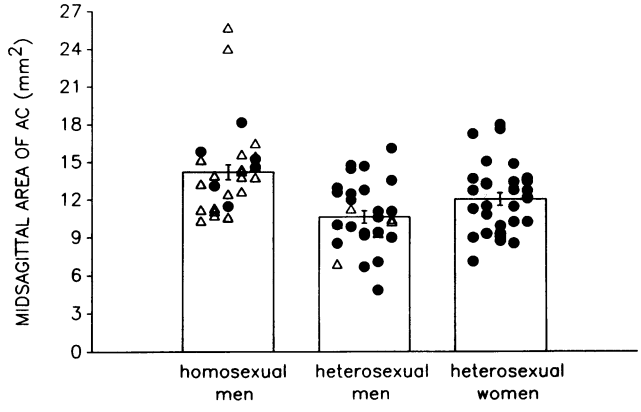

FIG. 1. Midsagittal area of the AC in homosexual men, heterosexual men, and heterosexual women. Data are means ± SEMs. Filled circles represent individual subjects without AIDS, and open triangles represent individual subjects who died of AIDS.

When the area of the AC in homosexual men without the two subjects with a relatively large AC is compared with the two heterosexual groups, a significant difference remains in the area of the AC and area adjusted for brain weight between heterosexual men but not heterosexual women (Table 1). Clearly, further studies are needed to determine whether the two large ACs represent a normal variation in homosexual men and whether the AC is, in fact, larger in homosexual men than heterosexual women. Although the AC size did not correlate significantly with brain weight ($r = 0.019$, $P = 0.86$) and the brain weights of homosexual and heterosexual men were similar, the brains of heterosexual females weighed significantly less than those of homosexual ($P < 0.0001$) and heterosexual ($P < 0.0001$) males. Therefore, we adjusted the size of the AC by dividing by brain weight. In this case, the AC of homosexual men was 36.0% greater than that of heterosexual men ($P = 0.0002$) but only 5.9% greater than that of heterosexual women ($P > 0.05$); the AC of heterosexual females was 28.4% greater than that of heterosexual males ($P = 0.003$). There was no difference between groups in postmortem period before autopsy or period between autopsy and photography. Apart from AIDS, there were no striking differences in terms of cause of death between the heterosexual groups.

Subjects who had AIDS included 24 homosexual males, 6 heterosexual males, and no females. ANOVA between men who did and did not die of AIDS indicated that the AC was significantly larger in homosexual than heterosexual men who died of AIDS ($P = 0.0116$) and in homosexual versus heterosexual men who did not die of AIDS ($P = 0.04$). However, within homosexual and heterosexual male groups,

Table 1. Area of AC at midsagittal plane of the brain, age, brain weight (BW), and area/BW for homosexual men, heterosexual men, heterosexual women, and homosexual men without the two subjects with markedly larger ACs

Group	n	Area, mm^2	Age, yr	BW, g	Area/BW, (mm^2/g) × 10^3
Homosexual men	30	14.20 ± 0.6*†	36.5 ± 1.4	1449 ± 22‡	10.1 ± 0.5¶
Heterosexual men	30	10.61 ± 0.5†a	38.7 ± 1.5	1439 ± 20§	7.4 ± 0.4¶‖c
Heterosexual women	30	12.03 ± 0.5*	39.7 ± 1.8	1275 ± 27‡§b	9.5 ± 0.4‖
Homosexual men-2	28	13.44 ± 0.4a	36.7 ± 1.4	1456 ± 22b	9.5 ± 0.4c

Data are mean scores ± SEMs. Symbol superscripts indicate comparisons between all groups; letter superscripts indicate comparisons between heterosexual men, heterosexual women, and homosexual men, excluding the two homosexual subjects with a markedly larger AC (homosexual men-2). Values with identical superscripts are significantly different at the indicated P level (Bonferroni t procedure): *, $P = 0.018$; †, ‡, §, and b, $P < 0.0001$; ¶, $P = 0.0002$; ‖, $P = 0.003$; a, $P = 0.0002$; c, $P = 0.0007$.

there was no significant difference between men who did and did not die of AIDS (Table 2).

In examining groups of all subjects and the three groups separately for correlations between the area of the AC, age, brain weight, postmortem period before autopsy, and period between autopsy and photography, the only significant correlations were between age and brain weight with age when all subjects ($r = -0.3024$, $P = 0.0038$) and heterosexual females ($r = -0.43$, $P = 0.017$) were examined.

In a previous study reporting a sex difference in the area of the AC in 100 age-matched male and female subjects, which were all different from those of this study, the AC was 12% greater in females than in males (16). Similarly, in this study when the areas of the AC in 60 age-matched heterosexual subjects are compared, we find a significant difference (one-tailed independent t test, $P = 0.022$), confirming our previous finding of a sex difference in area of the AC.

The accuracy of our measurements was limited by the precision by which a true midsagittal section was obtained and of the tracing of the AC in unstained tissue. In an ongoing study where tissue was sectioned coronally at 60 μm on a sliding microtome and stained with thionin, thereby permitting greater precision of measurements, a smaller sample size has actually revealed greater differences between the three groups, confirming the results of this study.

Although a majority of homosexual subjects in this study died of AIDS, there is no reason to believe that this disease resulted in an increase in AC area in these subjects. AIDS-related neuropathologies are predominately associated with neural atrophy. Moreover, neuropathology of structures connected by the AC, which may have not been specifically examined during autopsy, should also result in AC atrophy (30). However, two factors that can increase the size of a structure—local vacuolization and edema—were not apparent in any of the AC samples examined. Clearly, other histological preparations could indicate pathologies of the AC, but these would not be expected to increase the AC size. Furthermore, the AC is larger in homosexual than heterosexual men whether we compare subjects of both groups with or without AIDS (Table 2). Although individuals with AIDS show a high incidence of testicular dysfunction and lower serum testosterone levels (31, 32), and *decreased* circulating gonadal hormones result in *decreased* volumes of some sexually dimorphic nuclei (33–35), to our knowledge no study has examined the influence of circulating gonadal hormones on the morphology of structures other than sexually dimorphic nuclei. Nonetheless, no subjects in this study had medical records indicating testicular dysfunction. Although medical records were used to determine sexual orientation, heterosexual orientation was only assumed, rather than specified, in men and women who did not die of AIDS, hepatitis, or a disease associated with immunocompromise in young and middle-aged people. Clearly, subjects who were classified as heterosexual may not have been, and the degree of homosexuality or heterosexuality was unknown unless medical records indicated bisexuality. However, erroneous classification of subjects is likely to decrease chances of observing significant differences rather than resulting in apparent differences that do not exist.

Table 2. Area of AC at midsagittal plane of the brain for different groups

Group	n	Area, mm^2
Homosexual with AIDS	24	14.08 ± 0.16*‡
Homosexual without AIDS	6	14.65 ± 0.94†‡
Heterosexual with AIDS	6	9.63 ± 0.62*§
Heterosexual without AIDS	24	10.85 ± 0.57†§

Values (mean ± SEM) with superscripts that are the same indicate statistical comparison (Bonferroni t procedure): *, $P = 0.0116$; †, $P = 0.04$; ‡ and §, $P > 0.05$.

The AC of the primate brain is a tract of axons that primarily connects the right and left neocortex of the middle and inferior temporal lobes; fewer connections exist between the rostral superior temporal gyrus, olfactory complex, amygdala, and projections to the caudal superior temporal gyrus (36–41). Although subregions of several of these areas exhibit sexual dimorphism in various species, it is unknown whether sexually dimorphic structures in the human brain send or receive projections through the AC. Moreover, it is unknown whether differences in the area of the AC reflect differences in axon number, myelination, vasculature, connective tissue, or glia. In a small human sample, the area of the AC corresponded to the number of axons and not their density; however, in a study of rhesus monkeys, the midsagittal area of the AC did not correlate with the number of axons (42, 43). Although axonal elimination may occur due to atrophy with advancing age, in humans there is protracted myelination of the AC, at least into adulthood (44). Moreover, the size of the AC varies considerably within studies and the means of different studies vary (16, 42, 43, 45, 46). Age-related changes and considerable variation in AC area demonstrate a need for both age-matching and large-sample sizes.

The AC in monkeys may play a role in inhibiting bilateral formation of engrams, thereby increasing both functional asymmetry and pnemonic storage capacity of the brain by preventing redundancy (47). Monkeys with sectioned ACs could differentiate more accurately between left–right mirror images (48). In humans, the AC mediates the interhemispheric transfer of visual, auditory, and olfactory information (49).

The functional significance of differences in the area of the AC is unknown. However, differences in the connectivity between the cerebral hemispheres have been speculated to underlie sex differences between males and females in terms of cerebral lateralization (50, 51). Handedness, which may be a measure of cerebral lateralization, may correlate with sexual orientation (refs. 19–21; see also ref. 28), the size of regions of another fiber tract, the CC (51), and asymmetries of the temporal lobe (52). In fact, the region of the CC that varies with hand preference may contain fibers connecting asymmetric and sexually dimorphic regions of the temporal lobe (51). Moreover, there is a correlation between the size of the AC, sexual orientation, and scores on tests of verbal and visuospatial abilities and cerebral lateralization: homosexual men and heterosexual women have larger ACs, higher scores on verbal tests, and lower scores on exams of visuospatial abilities (23–26) and cerebral lateralization (27) than heterosexual men (also see ref. 29). However, handedness, determined by a questionnaire on hand preference for a variety of skills (19–21, 51) is not available in the medical records of these deceased subjects. It is currently unknown whether the AC connects asymmetric regions of the brain or whether its midsagittal area correlates with hand preference.

From studies of anatomical sex differences in the human brain (11–16), those differences that (appear to) relate to reproductive functions in which there is little overlap between men and women also exhibit relatively dramatic sex differences, in comparison to those that (appear to) relate to nonreproductive functions, such as cognition, in which considerable overlap occurs between males and females. Consistent with this observation, interstitial nucleus of the anterior hypothalamus 3, which is located in a region of the brain involved in reproductive function, exhibits more dramatic sex- (11) and sexual orientation-related (18) differences than the AC (16), which connects regions of the brain presumably involved in nonreproductive functions.

It is unknown at what period in life sex- and sexual orientation-related differences in the AC develop. However, in laboratory animals, a majority of neuroanatomical sexual dimorphisms arise during perinatal life, although more subtle changes in sexually dimorphic structures can also occur during adulthood (33–35). Because one cannot experimentally alter the hormonal environment of the developing human, it will be difficult to determine whether sexual differentiation of the human brain is influenced by gonadal hormones and/or is modified by environmental factors during fetal or neonatal life, as occurs in laboratory animals (50). However, knowledge of the time course of the establishment of structural sex differences in the human brain and the study of individuals exposed to atypical hormonal environments may be useful in identifying causal factors of homosexuality.

In vivo imaging techniques such as magnetic resonance imaging, which we used to confirm a sex difference in the shape of the corpus callosum in the living human (15), may be used to examine the relationship between sexually dimorphic brain structures and functions such as sexual orientation in both men and women, cerebral lateralization, and cognition—thereby including studies of homosexuals of both genders and eliminating problems with disease states and uncertain information regarding sexual orientation. The present report of a correlation between sexual orientation and the midsagittal area of the AC, a structure that is both sexually dimorphic and not believed to be related to reproductive function, when combined with reports of similar correlations with hypothalamic nuclei, clearly argues against the notion that a single brain structure causes or results from a homosexual orientation. Rather, this correlation supports the hypothesis that factors operating early in development differentiate sexually dimorphic structures and functions of the brain in a *global* fashion.

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