Handedness

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Handedness is described as an aspect of hemispheric specialization of function. This entry shows how hand-use, skill, and preference measures are more appropriate for examining the relation of handedness to other forms of hemispheric specialization of function (speech control, praxis, motor control mechanisms, sensorimotor foundations of cognition).

development   handedness   hemispheric specialization

1. Introduction

here is a general consensus among neuroscientists that the human left and right hemispheres of the brain have different perceptual, motor, emotional, and cognitive functions with the most distinctive difference of a left-hemisphere predominance in praxis (e.g., gestures and tool use) and language (speech and comprehension) functions [1]. However, many have argued that the phenomenon of hemispheric specialization of function is poorly specified as to what functions are separated between hemispheres and how functions interrelate both within a hemisphere and across hemispheres (e.g., [2,3]). In addition, the mechanisms that underlie these hemispheric differences in function are unclear (cf., [4]). Finally, there is little research focused on describing how the functional specialization of the hemispheres develops [5] or what role interhemispheric communication plays in that development. Thus, there is much opportunity for research.

2. Assessing Handedness

As McManus, Van Horn, and Bryden [1] note, handedness is "…that difference between the hands of which every right-hander and left-hander is **entirely aware** from their own behavior, but for which we have almost no adequate scientific explanation" (p. 394, emphasis added). For me, this definition of handedness aligns with only one method of handedness assessment, of which I count four. The **first** handedness assessment method is the most familiar and is associated with the human narrative identity ("I'm right-handed"). For most societies, handedness becomes a part of the person's identity similar to their sex, geographic locale (e.g., British, Parisian, Australian, Bostonian), familial ethnicity (e.g., Irish, Scandinavian, German, Italian, Persian, Thai, Taiwanese), etc. Like most forms of our narrative identity, the developmental precursors become observable during the second and third postnatal year and are marked by the production of such statements as "I am", "like me", etc. Therefore, the acquisition of symbolic language seems to be an important characteristic in the development of an individual's narrative or self-identified handedness. Once established, this handedness identity likely plays a role in the subsequent development of manual skills as children seek to make their skills concordant with their narrative identity.

Oddly, some societies have separate words for the right- and left-hand use (as in English), but they do not have a way of expressing a hand-use preference as part of their narrative identity (cf., [2][3][4]). Members can describe a preference for which hand they use for various manual activities (hammering, throwing, sewing with a needle, pulling the flesh while skinning an animal, etc.). Interestingly, the hand-use descriptive pattern that these societies use is very similar to a **second** method of assessing handedness: the self-report of the hand preferred for various manual actions (both unimanual and RDBM). This assessment method is represented by the 3 or 4 different questionnaires frequently used in neuropsychological research (e.g., the Edinburgh Handedness Index-EHI [5], the Waterloo Handedness Questionnaire-WHQ [6], Annett Questionnaire-AQ [7], Home Handedness Questionnaire-HHQ [8]).

Interestingly, the self-identity handedness fails to capture the individual variability that emerges when large samples of people are assessed via questionnaires. Indeed, the classification distribution for questionnaires is not as clearly categorical as that of self-identity (but see, [9]) and the more varied the manual tasks addressed by the questions (usually 10–15 tasks but can be as many as 60+), the more individual variability that can be expressed. Of course, there are statistical procedures that can reveal latent categories of people by identifying the associative patterns among the answers to the questions [9]. There may be three or more dimensions of handedness on which people may differ [10], but see [11]) or as many as eight handedness types [7] depending on the type of analysis used and the number of questions in the questionnaire [12].

The answers on a questionnaire are typically reduced to a single score, a laterality index (LI—(often (R − L)/(R + L) answers)). Interestingly, this LI (sometimes called a laterality quotient—LQ) can be used for various measures of hemispheric specialization of function from fMRI [13] to observational measures of handedness [1]. All too often, researchers choose an arbitrary cut-off score for the index in order to create most often two, but sometimes three categories (to capture ambilateral individuals) of people's handedness. These categories provide some consistency between the questionnaire and the narrative identity pattern. Unfortunately, problems arise because arbitrary cut-off scores can vary across studies making the categories established less reliable.

For example, although the typical LI ratio does not indicate whether the difference between the hands (or hemispheres) is significant, a categorical dominance classification is often imposed. A standard method of dominance classification for fMRI [13] uses cut-offs at +0.2 and −0.2 to divide left dominance (LI > +0.2) from bilaterality (−0.2 ≤ LI ≤ +0.2) and right dominance (LI < −0.2). Since such cut-offs are arbitrary, and Bradshaw et al. [13] found multiple studies that chose their own cut-off values, including 0.1, 0.33, 0.4, 0.5, and 0.6, using statistical classification techniques would provide some estimate of the reliability of the classification (e.g., for handedness, [14][15]; for fMRI, [16]). However, these techniques are seldom used (cf., [17]).

Indeed, variability in how handedness is assessed (e.g., parental report or measured hand-use preference), the type of handedness assessed (e.g., reaching or manipulation), methodology (ages of assessment, frequency of assessments, and time between assessments), and how the differences between the hands are defined [15][18] is likely to have contributed to the conventional notion that handedness is unreliable and unstable before 6–10 years of age [19]. However, defining a hand-use preference by a simple difference between hands (a "handedness index",

[20]) may create the impression that hand preferences are unstable across assessment ages. Whereas, defining a preference by statistical estimates of whether the intermanual differences are likely to have occurred by chance [15][21] can reveal consistent patterns [22][23].

The frequency of assessment during development also affects apparent handedness. Ferre et al. [22] reported that four bimonthly longitudinal assessments from 6 to 14 months of age show a different pattern of handedness development (no significant trend in hand-use preference) as compared to nine monthly assessments (a significant quadratic trend for right hand-use preference). Infant handedness is the consequence of an immature but rapidly developing nervous system that can be sensitive to different assessment procedures and conditions. Nevertheless, this does not mean that infant handedness is unreliable or even unstable or cannot be characterized.

Although questionnaires often show poor test-retest reliability [24], this can be improved psychometrically [25]. Indeed, using a psychometrically enhanced version of the EHI (and comparing it to a speed of finger-tapping performance task) and two taxometric procedures, Dragovic et al. [9] provided evidence that the distribution of hand preferences is discrete, not continuous. They found three categories of hand preference in large samples from two different geographic and demographic populations (Serbian teenagers and Australian adults): ~64% with "consistent right-handedness", ~29% with "inconsistent right-handedness", and ~7% with "consistent left-handedness". Hand preference was assessed using a shortened (only seven questions—drawing hand, upper hand on broom, and hand for lifting lid of a box were removed) but psychometrically enhanced EHI with better measurement properties [26].

Interestingly, one criticism of the EHI is that it is composed of actions, the majority of which are culturally dependent on Westernized tools [4]. Even a sample from a population in France had to have the broom question removed because so few participants had experience with a broom [27]. Nevertheless, the EHI is the most commonly used handedness assessment method in neuroscience research [28]. In addition, when used, it is often modified according to the purposes of the researcher, which can change its psychometric properties [28].

For example, Christman and colleagues (e.g., [29][30]) used neither a statistical nor a taxometric method with EHI scores to create a three-group classification procedure that distinguished "consistent right-handed", "consistent left-handed" and "inconsistent handed" (or "mixed-handed") individuals. They note that mixed-handed individuals are not ambilateral. Indeed, a "mixed-handed" individual could be someone who reports "always" using their right hand for 8 of the 10 EHI questions and "usually" using their right hand for one activity, and "always" using their left hand for the one remaining question. Thus, the "mixed-handed" group is likely to be more heterogeneous than the "consistent-handed" groups (a dodgy problem for statistical analysis). Then, they examined different relations of mixed-handed vs. consistent-handed individuals for many psychological functions (e.g., eating disorders and body image, gullibility, false memory, framing effects in cognitive decisions, Foreign language learning, episodic memory, paranormal beliefs). Some of these psychological functions are measured by a questionnaire, but some by empirical manipulations [29].

Since mixed-handedness (albeit not defined as in the Christman studies) is reported to be associated with a larger corpus callosum and presumably facilitates interhemispheric communication, Christman and colleagues posed a particular hypothesis about hemispheric specialization of function and interhemispheric communication to account for the observed relation of handedness to so many psychological functions. Their hypothesis [29] proposes a dual process pattern of hemispheric specialization with some psychological functions requiring mutually exclusive separation between hemispheres (e.g., the left hemisphere efficiently processes prototyped/abstract visual forms, whereas the right hemisphere efficiently processes exemplar/specific visual forms) and other functions require interhemispheric integration for effective functioning.

By re-examining several of their experiments, they [29] discovered that when dual processes must be integrated, mixed-handers are more affected by the experimental manipulations; whereas, if the processes are mutually exclusive (independent), then it is consistent right-handers who are more affected by the experimental manipulations. Christman and colleagues do note that the hemispheric specialization of some functions for consistent left-handed individuals is distinctly different from that of consistent right-handed individuals, but since consistent left-handers are such a small proportion of the population (~2–3% by their method of classifying handedness), they are considered too difficult to study and were ignored in the analyses ([29], footnote p. 3).

So, in order to reveal a relation of handedness to a very large variety of psychological functions, Christman and colleagues propose an elaborate theory about the relation of types of handedness (consistent right-handedness vs. mixed) to hemispheric specialization and interhemispheric communication. To derive the consistent verses mixed-handedness groups, they manipulate the EHI by using the absolute value of the LI scores, identifying the median (supposedly a score of 80), and then classifying individuals with absolute value scores of 75 or less as mixed-handed and those with higher scores as "consistent-handed". Using the median to construct groups is statistically troublesome, at best. At least, the classification technique of Dragovic et al. [9] might have been a more defensible procedure for specifying handedness groups. Even so, I would argue that the Christman method is not an adequate means of defining handedness groups, especially from the EHI scores. Therefore, the relation of handedness to such a variety of psychological functions needs replication and evaluation using more defensible ways of characterizing types of handedness. Indeed, I would apply this concern to nearly all studies that use questionnaire data to relate handedness to other psychological functions.

A **third** method of assessing handedness derives from observing preferred hand use during various manual actions. This reveals even more individual variability than the questionnaire assessment, probably because the self-report is biased by the individual's narrative identity and their desire to create cognitive consistency. In addition, the questionnaire may miss some aspects of manipulation that commonly occur in daily activities (self-grooming, gesturing, pulling/pushing oneself up from squatting, etc.). Observed handedness ought to bear some relation to hand differences in the gestural actions of infants and children (but see [31][32]). In addition, unless statistical procedures are used to reveal underlying groups of individuals with different patterns of hand-use expression [33], the variability is likely to be more continuously distributed among the members of the population.

The **fourth** assessment method examines differences between the hands in actual skilled activities. The measures include speed and accuracy differences between the hands or perhaps differences in leaning trials. There are various elements that make up manual skill, such as grip strength, finger dexterity, sequencing ability, and coordination across muscles, fingers, and hands. Each of these can be assessed by different functional tasks [34]. These measures can produce more precise descriptions of individual variability of hand-skill differences. Of course, this fourth method is affected by hand preference differences, which can lead to practice differences between each hand. Thus, skill differences have to be assessed with tasks that bear little resemblance to more highly practiced common manual actions (originally derived from hand-use preferences) with the hope that there are no simple transfer effects from the highly practiced actions to the relatively novel actions. Novel tasks are believed to identify the underlying processing differences between the hemispheres that produce the functional differences of handedness. However, even moving pegs from one set of holes to another nearby set likely involves transferred skills from other manual actions of grasping, relocating, and releasing an object. Perhaps that is why a GWAS and Annett's peg-moving task with over 2500 children and parents found that no SNP was associated with relative hand skill [35].

This fourth method ought to provide insight into the organization of the neural circuits that control different kinds of manual actions (e.g., finely-timed, serially ordered motor control of finger movements versus finely-timed, serially ordered motor control of shoulder, elbow, and wrist movements, or visually guided actions versus more ballistic or proprioceptive-guided actions). In addition, the assessments from this fourth method ought to correlate with praxis in neuropsychological functioning. Although the preferred hand is generally more skilled at performance-based tasks than the nonpreferred hand [36], McManus et al. [1] argue that measurements of performance, rather than reported preference, ought to be relied upon when investigating hemispheric specialization of function. Performance tasks likely tap into the neural mechanisms underlying lateralization of functions.

Several studies have used performance-based measures of preference, such as midline crossing tasks (e.g., [37]), to assess handedness. Midline crossing tasks measure the point at which reaching across the midline into contralateral (i.e., opposite) space with the preferred hand becomes too awkward, and participants switch to the nonpreferred hand to complete the task. Unfortunately, there is no agreed-upon set of novel tasks to measure the different aspects of hand differences in skill nor agreement on how to combine the speed and accuracy differences between the hands across tasks to create a general manual difference score. Moreover, since such performance tasks require the participant's comprehension of instructions and a motivation to perform the task as quickly and accurately as possible, this method is not appropriate for studying handedness development during infancy and early childhood. Finally, to date, this method has not incorporated any measure of RDBM (but see [38]), which may be the most important component of the expression of human handedness because so much of historical and even current tool manufacture and tool-using skills involve RDBM actions (e.g., [39]; see also, [40] about RDBM in professional musicians).

Comparison across each of these four methods of assessment results in too many individuals being classified differently [1][24]. A self-identified right-hander may become a weak left-hander by questionnaire, observed preference for use, or in measures of the differences in skill between the hands. Therefore, it is not surprising that

across studies, there would be differences in the association of handedness with other forms of hemispheric specialization. Indeed, some conclude (e.g., [41]) that genetic and neuroimaging studies in human adults have failed to support any causal relation between the direction of handedness and the lateralization of language. However, most studies assessing hemispheric specialization of function still use self-identity (sometimes checked by writing hand) or a questionnaire (most often the EHI) to assess handedness [28].

In the largest meta-analysis of handedness to date (over 2 million participants), Papadatou-Pastou et al. [42] converted each participant's handedness into a classification of Right-Mixed-Left (R-M-L), Right-Left (R-L), and Right-nonRight (R-nonR) in order to estimate the prevalence of left-handedness in the general population. Five meta-analyses measured (1) total left-handedness (irrespective of classification scheme), (2) non-right-handedness (from R-nonR classifications), (3) left-handedness from forced choice (from R-L classifications), (4) stringent left-handedness (from R-M-L classifications), and (5) mixed-handedness (from R-M-L classifications). Moderators for the analyses included comparing different measures of handedness (EHI, Annette's, self-description, writing hand, etc.), ancestry of participants (sub-Saharan Africa, European, East Asian), response format, year of publication, education of participants, and mixed-handedness (from R-M-L classifications).

They found no evidence of relevant differences in prevalence estimates for left-handedness based on writing hand assessment as compared to self-classification or assessment with most questionnaires. The proportion of left-handedness was found to be about 17% for nonR-R classification schemes, 10% for R-L classifications, and 9% for R-M-L classifications. Mixed-handedness also represented about 9% of the population. Ancestry affected the prevalence of left-handedness, with Europeans having the greater proportion (11%). Males were consistently more likely to be left-handed than females, and increased education increased left-handedness. The authors conclude that a shorter questionnaire or even writing hand can be used to assess handedness. In contrast, I would argue that questionnaires are not adequate means for assessing handedness if the intent is to relate handedness to sensorimotor control mechanisms.

A recent study [1] compared performance differences between hands using the Tapley and Bryden task (TBT) of dotting inside sequences of "Os" and the Annett pegboard task (APT) and related these performance differences to the scores on a modified EHI and self-described handedness. When classified into groups, the distribution of LI scores on the mEDI was highly correlated with self-described handedness. I would interpret this result as the need of adult subjects to make their questionnaire answers consistent with the narrative identity of their handedness. McManus et al. [1] also reported that despite the T and B performance task being a very suitable measure of direction (R or L) of handedness, it is not a suitable measure of the degree of handedness. They conclude that the differences between left- and right-handers versus those differences between strong and weak left-handers (or strong and weak right-handers) are the result of the processes from different underlying mechanisms. As yet, there is no evidence for these different mechanisms.

However, it is likely that the neural mechanisms associated with controlling the sensorimotor skills involved with the actions that create handedness differences in performance or preference for use are different from those associated with self-identity or language-dependent questionnaire accounts of handedness, both of which depend

upon declarative memory. I would argue that the neural mechanisms associated with identity and self-report assessments would bear little relation to those associated with the production of speech (a sensorimotor process that is more similar to the control of the hands). Therefore, I would not expect identity handedness to be related to measures of speech production and decoding.

Hickok and colleagues [43][44][45] also argue that the neural circuits involved in speech production and decoding are different from those involved with processing the conceptual-semantic aspects of speech. They propose that the processes used to produce speech (and decode it before subsequent semantic analysis) are associated with circuits that are involved with other sensorimotor processes. Indeed, there appear to be neural circuits that support the interface between auditory and motor processing of speech similar to those involved with sensory-motor integration. These supramotor functions (e.g., sequencing actions and the precise timing of muscle contractions and relaxations) are not specific to speech but underlie all action preparation [46].

Many models of speech motor planning propose that speech derives from common action control and motor-sequencing mechanisms that also underlie many other cognitive processes [47][48]. Therefore, the neural organization of speech production is likely to overlap with those motor control regions likely involved with manual differences in those skills associated with handedness. For example, Broca's area is associated with many nonlanguage motor functions, including planning actions, imitating actions, and using tools [49][50]. Therefore, if handedness is to be related to hemispheric specialization for speech production, we need to focus on differences in hand preference or skill, not narrative identity or questionnaire scores [51]. For example, Packheiser et al. [52] found no association between lateralization for language (as measured by ear differences in dichotic listening) and handedness for over 1500 adults. Handedness was measured by the EHI using four common classification schemes, including one based on latent class analysis.

The sequencing of speech motor acts and the organizing of segmental information into words and sentences prior to vocalizing relies more heavily on the motor areas. Interruption of these motor regions via transcranial magnetic stimulation (TMS) has been shown to disrupt sequencing actions on a finger-tapping task and to impair the performance of oral motor gestures [53]. Such results suggest that the cortical organization of motor and speech networks may be complementary [54]. Studies also show a clear role for the cerebellum and basal ganglia in translating motor planning into action for speech and manual actions [48], and deficits in cerebellar-parietal networks occur in children with developmental coordination disorder (DCD—[55]). Therefore, to understand the manifestation of handedness, it is important to understand the neuroscience of forelimb movements.

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