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Sinistrals' upper hand: Evidence for handedness differences in the representation of body space

Sylvia Hach *, Simone Schütz-Bosbach

Max Planck Institute for Human Cognitive and Brain Sciences, Germany

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ABSTRACT

A difference in the perception of extrapersonal space has been shown to exist between dextrals and sinistrals. On the classical line bisection task, this difference is evident in a greater left bias for dextrals compared to sinistrals. Different modalities and regions of space can be affected. However, it has not yet been investigated whether a systematic bias also exists for the perception of personal or body space. We investigated this by using three tasks which assess different aspects of personal space in an implicit and explicit way. These tasks were performed by strongly right-handed (dextrals), strongly left-handed (sinistrals) and mixed-handed participants. First, a task of pointing to three areas of one's own body without the use of visual information showed dextrals to have an asymmetric estimation of their body. In right hemispace, dextrals' pointing was at a greater distance from the midsagittal plane compared to pointing in left hemispace. No such asymmetry was present for sinistrals, while mixed-handers' performance was intermediate to that of strong right- and strong left-handers. Second, a task of recovering circular patches from their body surface whilst blindfolded also showed superior performance of sinistrals compared to dextrals. On these two tasks, there was also a moderate relationship between handedness scores and performance measures. Third, a computer-based task of adjusting scaled body-outline-halves showed no handedness differences. Overall, these findings suggest handedness differences in the implicit but not explicit representation of one's own body space. Possible mechanisms underlying the handedness differences shown for the implicit tasks are a stronger lateralization or a greater activation imbalance for dextrals and/or greater access to right hemispheric functions, such as an "up-to-date body" representation, by sinistrals. In contrast, explicit measures of how body space is represented may not be affected due to their relying on a different processing pathway.

1. Introduction

Right- and left-handers (dextrals and sinistrals, respectively) differ most obviously with respect to their upper limb preference (Goble & Brown, 2008). In the course of three waves of studies investigating the origin of handedness and its association with the symmetry of hemispheric functioning, a range of other differences have also been identified (Hatta, 2007). For example, handedness differences in visuospatial abilities have been cited frequently, and spatial ability has been found to decline with increasing dextrality (Annett, 2002). These differences are thought to arise from differential lateralization, with dextrals showing a greater and sinistrals a lesser degree of such (e.g., Knecht et al., 2000; Szaflarski et al., 2002). With regard to a representation of external space, it is thought that the right hemisphere of dextrals directs attention to ipsi- *and* contralateral space, leading to an overrepresentation of the right hemispace in comparison to the left hemispace (Corbetta, Miezin, Shulman, & Petersen, 1993). Sinistrals, in contrast, appear to represent external space comparatively evenly (Bowers & Heilman, 1980; Luh, 1995; Sampaio & Chokron, 1992). This asymmetry in spatial representation found in right-handers is termed 'pseudoneglect', with reference to neglect sufferers who disregard left hemispace as a result of right parietal lesions. Whether handedness differences also exist for the representation of other spatial compartments such as the representation of one's body (termed personal or body space here) is not yet known. The aim of the present study was to contribute to answering this question. This is also relevant for our understanding of how far the representation of one's body is modulated by individual factors.

Human lesion and animal studies have identified the right parietal cortex to be the main neural locus of spatial processing (Driver & Vuilleumier, 2001; Husain & Nachev, 2006; Pouget & Driver, 2000). Not only can lesions in this part of the cortex lead to a disregard of the contralesional space which closely surrounds the sufferer (peripersonal space), but most strikingly also to a complete

* Corresponding author. Address: Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstr. 1a, 04103 Leipzig, Germany. Fax: +49 341 9940 2204.
E-mail address: hach@cbs.mpg.de (S. Hach).

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disregard of the contralesional side of the sufferer's body (personal or body space). For example, these patients may comb their hair, shave or dress only the non-affected right side of their body (e.g., Bisiach, Perani, Vallar, & Berti, 1986). This form of personal neglect can occur without affecting the representation of extrapersonal space (i.e., space beyond manual reaching distance) but the opposite pattern can also arise. That is, neglect affecting extrapersonal space can be dissociated from personal or peripersonal neglect syndromes (e.g., Halligan & Marshall, 1991; Ortigue, Megevand, Perren, Landis, & Blanke, 2006; Vuilleumier, Valenza, & Mayer, 1998). This dissociation suggests a different functional and neuroanatomical basis of personal/body space – the space that our own body itself occupies – and extrapersonal space – the space that surrounds our body (Committeri et al., 2007).

Evidence from both animal and patient studies suggests that the parietal cortex is also crucially involved in the representation of personal or body space (Colby & Duhamel, 1996; Graziano & Cooke, 2006). A recent lesion study that investigated a large sample of right hemisphere stroke patients, for example, found the inferior parietal cortex including the supramarginal and post-central gyrus as well as the medial white matter to be selectively implicated in neglect of personal space (Committeri et al., 2007). In contrast to neurons in the primary somatosensory brain regions, neurons contained in parietal regions are multimodal. That is, they respond to tactile, visual and/or auditory stimuli delivered on or close to the body. Therefore, lesions in this brain region can lead to personal neglect in different sensory modalities even though the primary somatosensory areas of the brain are intact (e.g., Bisiach & Vallar, 2000). In addition, personal neglect can be the result of a functional disconnection between primary regions for coding proprioceptive and somatosensory input and regions coding a more abstract spatial representation of the body (Committeri et al., 2007). In line with this assumption, studies that investigated patients with autotopagnosia (i.e., patients who make mislocalization errors when asked to point to specific body parts) also suggested that the inferior parietal lobe plays a key role in maintaining spatial relationships of body parts (e.g., Buxbaum & Coslett, 2001; Ogden, 1985; Sirigu, Grafman, Bressler, & Sunderland, 1991).

In recent years, several studies have suggested that the right hemisphere in particular, or more specifically, the right inferior parietal lobe, appears to subserve a spatial representation of one's own body (e.g., Blanke, Landis, Spinelli, & Seeck, 2004; Bottini, Bisiach, Sterzi, & Vallar, 2002; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Vallar & Ronchi, 2009). Interestingly, it has also been suggested that people who are not strongly right-handed have better functional access to right hemisphere processing across different domains such as attention, decision making or memory (e.g., Annett, 2002; Christman, Jasper, Sontam, & Cooil, 2007; Propper, Christman, & Phaneuf, 2005). Functional access in this case refers to the recruitment of specialized neural structures for performance on a task that is high on the demands of this particular ability and 'better functional access' results from greater neural interconnectivity (higher number of white matter tracts/synapses) (He et al., 2007).

Therefore, one can ask whether people who are not strongly right-handed perhaps also have better access to and thus a more precise structural representation of their own body, which is assumed to be located in the right hemisphere. This question has in fact been addressed by Niebauer, Aselage, and Schutte (2002), who compared the susceptibility to the so-called rubber hand illusion in strong right-handers and less strongly right-handed participants. Remarkably, the authors found that the latter participant group indeed reported a stronger experience and a tendency to a faster onset of the illusionary experience of incorporating a fake hand into their body schema after observing the fake hand being stroked in synchrony to their own occluded hand. The authors proposed that due to the assumed greater right hemisphere access, the less strongly handed were more "efficiently" able to update their body representation and thus experience the illusion to a greater extent. However, this study did not directly test whether strong right-handers generally represent their own body differently as the present study aims to do.

At this point it has to be noted, however, that a great heterogeneity of terms are used in the handedness literature. While a number of original studies conceptualized handedness in terms of direction (right versus left), most of the recent behavioral literature contrasts the performance of strong (right)-handers with that of mixed-handed participants (e.g., Christman, Bentle, & Niebauer, 2007; Christman & Jasper et al., 2007). The assumption here is that in strong right-handers (who use their dominant hand for every task), the two hemispheres operate more independently. This contrasts with the two hemispheres operating in a more integrative manner in moderate right-handers (also called mixed-handers by some authors) (e.g., Knecht et al., 2000), who use their dominant hand for some, but not all everyday tasks, ambidextrous and strong left-handers. In fact, strong left-handers are often excluded from these studies (e.g., Christman & Bentle et al., 2007; Christman, Henning, Geers, Propper, & Niebauer, 2008). This, in turn, stands in contrast to even very recent functional brain studies which mostly study handedness in the right–left dichotomous fashion (e.g., Iwabuchi & Kirk, 2009; Rocca, Falini, Comi, Scotti, & Filippi, 2008).

The present study aimed at investigating behavioral differences between a group of strongly right-handed participants, a group of mixed-handed participants and a population previously neglected in behavioral studies, that of strongly left-handed participants. Handedness is considered, both in terms of direction and in terms of degree. That is, in contrast to the literature presently available, the current study includes analyses of behavioral measures in terms of a trichotomy of handedness (right-, mixed- and left-handed participants) and in terms of contrasting strong (right- and left-handed participants combined) with mixed-handers. More specifically, the present study investigates body representation in relation to handedness and is to our knowledge the first to do so. Three different tasks were employed to achieve this.

In the first task, we asked our three participant groups to indicate points on their left and right body outline (i.e., shoulder, waist and hip) without using visual information. This task provides an implicit test of how body space is represented in the horizontal dimension and is processed presumably by more automatic sensorimotor loops as indicated by, for example, "blind touch". Blind touch refers to the phenomenon of patients who are able to correctly point to and thus localize stimuli on their body of which they are not explicitly aware (Gallace & Spence, 2007; Paillard, 1999; Paillard, Michel, & Stelmach, 1983; Rossetti, Rode, Farne, & Rossetti, 2005). That is, pointing to one's own body, as for the completion of this first task, may occur independently of immediate or explicit awareness of one's own bodily dimensions and therefore represent an implicit test of body representation.

As a second test, we used a modified version of the so-called Fluff Test which was originally developed and reported by Cocchini et al. (2001). So far, this test has only been used in the clinical context to assess personal neglect syndromes in neurological patients. It involves the placement of 24 stimuli on the patient's body (i.e., on the torso, arms and legs) while he or she is blindfolded. The patient is then required to remove all stimuli from his or her body. Patients suffering from personal or body space neglect typically detect these stimuli on the ipsilesional right side of their body only. This test also provides an implicit test of body structure as it requires the haptic localization of the stimuli with reference to an overall representation of the body that provides the spatial field in which the stimuli can be detected. In the present study, we