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Differential effects of galvanic vestibular stimulation on arm position sense in right- vs. left-handers

Lena Schmidt [a,b,*], Frank Artinger [c], Oliver Stumpf [c], Georg Kerkhoff [a,b,*]

[a] Saarland University, Clinical Neuropsychology Unit and Outpatient Service, Saarbruecken, Germany
[b] International Research Training Group 1457 "Adaptive Minds", Saarbruecken, Germany
[c] University of Applied Sciences, Faculty of Mechanical Engineering and Mechatronic, Karlsruhe, Germany

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ABSTRACT

The human brain is organized asymmetrically in two hemispheres with different functional specializations. Left- and right-handers differ in many functional capacities and their anatomical representations. Right-handers often show a stronger functional lateralization than left-handers, the latter showing a more bilateral, symmetrical brain organization. Recent functional imaging evidence shows a different lateralization of the cortical vestibular system towards the side of the preferred hand in left- vs. right-handers as well. Since the vestibular system is involved in somatosensory processing and the coding of body position, vestibular stimulation should affect such capacities differentially in left- vs. right-handers. In the present, sham-stimulation-controlled study we explored this hypothesis by studying the effects of galvanic vestibular stimulation (GVS) on proprioception in both forearms in left- and right-handers. Horizontal arm position sense (APS) was measured with an opto-electronic device. Second, the polarity-specific online- and after-effects of subsensory, bipolar GVS on APS were investigated in different sessions separately for both forearms. At baseline, both groups did not differ in their unsigned errors for both arms. However, right-handers showed significant directional errors in APS of both arms towards their own body. Right-cathodal/left-anodal GVS, resulting in right vestibular cortex activation, significantly deteriorated left APS in right-handers, but had no detectable effect on APS in left-handers in either arm. These findings are compatible with a right-hemisphere dominance for vestibular functions in right-handers and a differential vestibular organization in left-handers that compensates for the disturbing effects of GVS on APS. Moreover, our results show superior arm proprioception in left-handers in both forearms.

1. Introduction

The human brain is characterized by an asymmetrical organization, consisting of two hemispheres with different functional specializations. For many years, researchers have used handedness as an indirect indicator of cerebral specialization (Amunts et al., 1996; Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009; Witelson, 1989).

1.1. Lateralization of sensory-motor functions in left- vs. right-handers

In general, motor functions are probably more strongly lateralized than emotional, cognitive or sensory abilities (Gutwinski et al., 2011). Moreover, right-handed individuals rely more on their dominant, right hand as compared to left-handers who rely more on both hands (Gonzales, Whitwell, Morrissey, Ganel, & Goodale, 2007; Linkenauger, Witt, Stefanucci, Bakdash, & Proffitt, 2009). In line with this, cortical representations of the right arm and hand are greater in the left hemisphere of right-handers, whereas left-handers represent these body parts in a more symmetrical fashion in both hemispheres (Linkenauger, Witt, Bakdash et al., 2009). While right-handers show a left-hand advantage for global judgments and a right-hand advantage for local judgments in haptic processing, left-handers exhibit a weaker asymmetry in such bimanual tasks (Tomlinson, Davis, Morgan, & Bracewell, 2011). Gardner and Potts (2010) showed that hand dominance also influences the performance in an own

Abbreviations: APS, arm position sense; GVS, galvanic vestibular stimulation; R-GVS, right-cathodal/left-anodal; L-GVS, left-cathodal/right-anodal; APD, arm position device; AE, after-effect; UE, unsigned errors; CE, constant errors

* Corresponding authors at: Saarland University, Clinical Neuropsychology Unit and Outpatient Service, Building A.1.3., D-66123 Saarbruecken, Germany. Tel.: +49 681 302 57385, +49 681 302 57380; fax: +49 681 302 57382.
E-mail addresses: lena.schmidt@mx.uni-saarland.de (L. Schmidt), kerkhoff@mx.uni-saarland.de (G. Kerkhoff).

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body transformation task. They found an attentional bias toward the side of the observed body that corresponds to the dominant hand of the participants, suggesting a modulatory effect by handedness even in imagined perspective transformations. Hach and Schütz-Bosbach (2010) found evidence for handedness differences in the implicit but not explicit representation of body space and the authors interpreted this result by a greater lateralization in dextrals.

Structural and functional imaging studies corroborate these behavioral results in showing a different organization of the left/right central sulcus (Amunts et al., 1996), the somatosensory cortex (Buchner, Ludwig, Waberski, Wilmes, & Ferbert, 1995), and the parietal lobe (Devlin et al., 2002; Perenin & Vighetto, 1988) in right- vs. left-handers. In a fMRI study concerning hemispheric specialization for praxis, Vingerhoets et al. (2012) found similar lateralized activation patterns for pantomiming learned movements in left- and right-handers but a reduced strength of asymmetries predominantly in the posterior parietal cortex in left-handers. In sum, previous studies suggest stronger structural and functional asymmetries in right-handers as compared to left-handers who show a more symmetrical organization resulting in less asymmetry in sensorimotor tasks performed with the left or right hand.

1.2. Cortical vestibular system

The vestibular system is involved in mental timing (Binetti, Siegler, Bueti, & Doricchi, 2012), the recognition of the own body position in space as well the determination of movement in space (Dieterich, 2006), in somatosensory processes (Dijkerman & De Haan, 2007; Ferrè, Sedda, Gandola, & Bottini, 2011; Vallar, Bottini, Rusconi, & Sterzi, 1993) and motor functions (Rode, Perenin, Honoré, & Boisson, 1998; Rode et al., 2012). It acts as a basic reference system for the other sensory systems, provides information about spatial orientation and operates in egocentric and allocentric reference frames (Eickhoff, Weiss, Amunts, Fink, & Zilles, 2006). The vestibular system entails a highly organized thalamo-cortical projection (for a review see Lopez & Blanke, 2011). Functional imaging studies of the vestibular system using galvanic vestibular stimulation (GVS; Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Lobel, Kleine, Bihan, Leroy-Willig, & Berthoz, 1998) or caloric vestibular stimulation (Bottini et al., 1994) have revealed a network of vestibular areas including the temporal, parietal and insular cortices, as well as the putamen and thalamus, which is distributed in both cerebral hemispheres, but with a right-hemispheric dominance in right-handers (Brandt & Dieterich, 1999; Bense et al., 2001; Suzuki et al., 2001). Recent studies complement these findings by showing that vestibular activations in right- and left-handers are stronger in the hemisphere ipsilateral to the preferred hand (Janzen et al., 2008) and showing that vestibular stimulation is based on opioid neurotransmission which is pronounced in the right hemisphere in right-handers (Baier et al., 2010).

Few studies have so far investigated the vestibular network in left-handers. In a PET study of Dieterich et al. (2003), the effects of caloric vestibular stimulation on vestibular activation in 12 right-handed and 12 left-handed individuals were investigated. In both handedness groups they found significant activations in both hemispheres, both subcortically in the putamen, thalamus and midbrain, as well as cortically in frontal and temporo-parietal areas and the posterior insula. These activations were bilateral, but with a preponderance of the non-dominant hemisphere: in right-handers the right hemisphere, in left-handers the left hemisphere was stronger activated. Dieterich et al. (2003) concluded that cortical and subcortical activations induced by caloric vestibular stimulation depend on handedness. In their view, vestibular lateralization determines right- or left-handedness, because the vestibular system matures earlier during ontogeny while handedness and language lateralization occur later (Dieterich et al., 2003). There is also evidence that prenatal asymmetry of the vestibular development, among others, may influence handedness and cerebral lateralization because left-otolithic dominance may induce right-sided motoric dominance and a right-hemisphere specialization for visuo-spatial functions (for a general review see Previc, 1991).

1.3. Arm position sense

Proprioception or limb position sense is an important capacity to locate one's own limbs without visual feedback. Impaired position sense leads to imprecise motor functions, reduced spontaneous use of arms, awkward limb positions, reduced safety and postural instability (Dijkerman & De Haan, 2007). Disturbed limb position sense in space or in relation to their own body is frequent in patients with stroke, e.g. of the arm (further named APS=arm position sense; Vallar, Antonucci, Guariglia, & Pizzamiglio, 1993; Vallar, Guariglia, Magnotti, & Pizzamiglio, 1995; Schmidt et al., in press). Moreover, contralateral APS disorders were more frequent and severe in right brain-damaged patients, especially those with left neglect (Pizzamiglio, Frasca, Guariglia, Incoccia, & Antonucci, 1990; Schmidt et al., in press; Sterzi et al., 1993; Vallar, Antonucci et al., 1993, Vallar, Guariglia et al., 1995). Furthermore, there is a close relationship between vestibular cortical projections and hand/arm representations in the central sulcus (Robertson, Tegnerér, Goodrich, & Wilson, 1994).

1.4. Rationale of the present study

In light of the above-mentioned greater behavioral and anatomical asymmetries in right- vs. left-handers and their differential vestibular brain organization one might expect behavioral asymmetries in APS of the two forearms in left- and right-handers, as shown for other sensorimotor tasks. Moreover, both handedness groups should respond differentially to vestibular stimulation when performing APS. As the cortical vestibular system is dominantly organized in the right parieto-temporal cortex in right-handers (see above), and right-cathodal/left-anodal GVS (further named R-GVS) leads to an activation of the right vestibular cortex (Fink et al., 2003) this GVS condition should have differential effects on arm position sense in right- and left-handers. In a previous study, we found, as an unexpected side effect, that R-GVS disrupts left APS in right-handers (Schmidt et al., in press). Therefore, we expected in the present study, that R-GVS should disrupt left APS in right-handers, but should have no or less disruptive effects in left-handers. In contrast, left-cathodal/right-anodal GVS (further named L-GVS) might disrupt right APS in left-handers, because of their dominant organization of the vestibular system in the left hemisphere. Alternatively, GVS should have no disturbing effect on APS in left-handers at all, because of their more pronounced *bilateral* vestibular organization.

The present study, therefore, aimed to study the handedness-specific hemispheric lateralization of vestibular functions, with the following questions and hypotheses:

(i) Does APS accuracy of left- and right-handers differ, respectively in the left and right arm, as shown for other motor tasks? We expected that left-handers are more accurate in the APS of *both* arms, whereas right-handers should show a greater right-left asymmetry (see Section 1).

(ii) Does GVS modulate the APS in healthy left-handers in a similar way as shown for right-handers (Schmidt et al., in