



Hemispheric asymmetries of a motor memory in a recognition test after learning a movement sequence



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ABSTRACT

Two experiments utilizing a spatial-temporal movement sequence were designed to determine if the memory of the sequence is lateralized in the left or right hemisphere. In Experiment 1, dominant right-handers were randomly assigned to one of two acquisition groups: a left-hand starter and a right-hand starter group. After an acquisition phase, reaction time (RT) was measured in a recognition test by providing the learned sequential pattern in the left or right visual half-field for 150 ms. In a retention test and two transfer tests the dominant coordinate system for sequence production was evaluated. In Experiment 2 dominant left-handers and dominant right-handers had to acquire the sequence with their dominant limb. The results of Experiment 1 indicated that RT was significantly shorter when the acquired sequence was provided in the right visual field during the recognition test. The same results occurred in Experiment 2 for dominant right-handers and left-handers. These results indicated a right visual field left hemisphere advantage in the recognition test for the practiced stimulus for dominant left and right-handers, when the task was practiced with the dominant limb.

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1. Introduction

Liepmann's (1905) seminal paper on lateralization of the human motor system has stimulated the research of functional asymmetry in the two human brain hemispheres. Based on post-mortem findings Liepmann proposed that the left hemisphere is primarily responsible for controlling movements (see also Serrien, Ivry, and Swinnen, 2006). In the years following the completion of Liepmann's work neuroscientists, psychologist, and researchers in motor control and learning began systematically studying hemisphere differences in the control of movements (e.g. Aziz-Zadeh, Iacoboni, Zaidel, Wilson, and Mazziotta, 2004; Haaland and Harrington, 1989; Kimura, 1977; Mutha, Haaland, and Sainburg, 2012; Sainburg, 2005), and more recently in movement sequence learning (Ellenbuenger et al., 2012; Keele, Ivry, Mayr, Hazeltine, and Heuer, 2003; Schmitz, Pasquali, Cleeremans, and Peigneux, 2013; Shea, Kovacs, and Panzer, 2011; Serrien and Sovijärvi-Spapé, 2015; Shea, Panzer, and Kennedy, 2016).

Research related to behavioral and neurophysiological experiments and results from brain damage patients with left or right hemisphere lesions have provided strong empirical evidence for hemisphere specialization in the control of movements (Haaland and Harrington, 1989; Harrington and Haaland, 1992; Kimura, 1977; Mutha et al., 2012; Serrien et al., 2006 for overviews). That is, in dominant right-handers

the left hemisphere is specialized for the control of movements in both limbs (Haaland and Harrington, 1996). These results corroborated the earlier findings from Liepmann (1905).

Experimental investigations using the inter-manual transfer design to study the hemisphere/limb specialization system in healthy individuals have indicated transfer asymmetry. A basic assumption was that the hemisphere/limb specialization limits the development and/or utilization of one or more representations for response production depending on which limb is used during the course of learning and later used in the transfer tests. The transfer direction of reaching movements, for example, was superior from the non-dominant to the dominant limb when movement dynamics (limb trajectory) had to be controlled whereas transfer from the dominant to the non-dominant system was more effective when the end-position of the limb (limb position) had to be controlled (Sainburg, 2005). To account for the asymmetry associated with effector transfer several theoretical models have been proposed (Hicks, 1974; Parlow and Kinsbourne, 1989; Taylor and Heilmann, 1980; see Mutha et al., 2012; Thut et al., 1996, for overviews). Each of these theoretical perspectives was based on notions of functional specialization of the two hemispheres and the crossed pathways of the limb motor system argues that each hemisphere exhibited different specializations and task specific characteristics in controlling movements of each limb. The left hemisphere (LH) is involved in processing movement dynamics and torques whereas the right hemisphere (RH) is responsible for the visual-spatial environment and is implicated in the development of a spatial memory (Gooijers and Swinnen, 2014; Goldberg, Podell, and Lovell, 1994; Schumacher, Elston, and D'Esposito,

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2003). Recently research investigating the neural mechanisms on lateralization and the control of movement sequences with left- and right-handers provided strong empirical evidence that in both groups the LH is specialized in the organization and execution of movement sequences (Serrien and Sovijärvi-Spapé, 2015), which suggested that the hemispheric asymmetry for controlling movement sequences is independent of hand preference.

An alternative approach to determine the role of hemispheric specialization for the memory of the task specific information is by using a recognition test in different visual half-fields. The basic assumption of the visual half-field (VHF) presentation is based on inter-hemispheric transmission and the physiological structures of the crossed visual pathways that visual stimuli presented selectively to either the left visual field (LVF) or the right visual field (RVF) is projected directly to the contralateral hemisphere (Bourne, 2006). The logic behind the VHF paradigm is that a stimulus projected directly to one hemisphere is initially perceived and processed in this hemisphere, and is more amenable for information processing. According to the functional hemisphere differences and lateralized processing, reaction time is shorter when information first reaches the specialized hemisphere, because the perceived information has not been transmitted through the corpus callosum to the specific hemisphere (Hardyck, Tzeng, and Wang, 1977; Kinsbourne, 1970; Poffenberger, 1912; Berlucchi, Aglioti, and Tassinari, 1994 for a review). Much of the earlier experiments which have used the VHF paradigm were done in the verbal domain. This work provided strong empirical evidence that verbal material is lateralized to the left hemisphere (Aziz-Zadeh, Koski, Zaidel, Mazziotta, and Iacoboni, 2006).

Experiments using the VHF-paradigm in the context of movement sequence learning have provided evidence for hemispheric specialization in the development of a sequence representation (Ellenbuenger et al., 2012; Schmitz et al., 2013). In an observational learning experiment, Ellenbuenger et al. (2012) combined the VHF paradigm and the inter-manual transfer paradigm. The main purpose of their experiment was to determine the impact of the development of an efficient representation for sequence production following observational training in different visual half-field conditions on later physical performance of a spatial-temporal sequence. Participants were instructed to observe a video model during the learning of a movement sequence. The video model was presented in the LVF, central position or in the RVF to the participants. To determine the representation used in the coding of the sequence during observational practice participants were instructed to perform the sequence physically in two effector transfer tests after a rest interval. In one effector transfer test the motor coordinates were reinstated such that the participant had to reproduce the same pattern of muscle activations with the contralateral limb (homologous muscles) as was utilized during acquisition. Therefore the visual display was presented in a mirror image. The other effector transfer test required participants to reproduce the same spatial positions (non-mirror image) of the targets as experienced during the acquisition phase. By changing to the unpracticed limb, the participant has to produce a new pattern of activation of the muscles to achieve the target positions. Participants of the central position- and LVF-groups demonstrated an inter-manual transfer advantage to the non-mirror image compared to the participants of the RVF-group, which did not promote a specific transfer pattern. However, visual-spatial information was the only source of information for participants to acquire a movement representation, because they had no direct access to motor related information while observing during acquisition. The conclusion was that observing the movement sequence in the LVF increased processing of information to develop an effective visual-spatial representation for later sequence execution compared to the RVF and that this information is primarily represented in the right hemisphere. This finding is in accordance with the assumption that the right hemisphere is involved in the development of a spatial representation (see Schumacher et al., 2003).

The result of the experiment was also consistent with the 'Parallel network model' proposed by Hikosaka et al. (1999). Based on this

model the processing of a movement sequence is distributed in the brain in independent spatial (e.g., spatial locations of end effectors and/or sequential target positions) and motor coordinates (e.g., activation patterns of the agonist/antagonist muscles and/or the sequence of joint angles) with distinct neural networks subserving each class of processing. According to this perspective sequence learning involved both, a fast developing, effector independent component represented in visual-spatial coordinates and a slower developing effector dependent motor component that is represented in motor coordinates (see also de Kleine and Verwey, 2009). In addition, the Hikosaka perspective also proposed that codes based on visual-spatial and motor coordinates developed in parallel, while the preference of one code for sequence production depends on the stage of practice, and/or the available feedback provided during sequence execution (Leinen, Shea, and Panzer, 2015).

To dissociate hemisphere specialization of memory processes and motor execution Jason (1983) instructed patients with a left sided lesion and patients with a right sided lesion, to execute and to remember a manual sequence task of different hand positions. By systematically varying the memory or the motor demands of the task, he demonstrated that the left sided lesion patients performed worse when executing the task compared to the right sided lesion patients. In remembering the task both patient groups performed on the same level. However, all patients could choose if they used their left or right hand. Therefore it is entirely possible that the longer execution times from the left sided lesion patients resulted from the hand used for executing the task rather than from functional hemispheric differences.

Whereas previous work on sequence representation and lateralization has predominantly focussed on transfer-direction and motor output performance to investigate cerebral hemispheric specialization of visual-spatial or motor information, little attention has been directed to the question of the lateralization of the memory of the motor sequence. This is interesting because the research on movement sequences has led to a number of theoretical models (e.g., Keele, Jennings, Jones, Caulton, and Cohen, 1995; Klapp, 1996; Rosenbaum, 1990; Schmidt, 1975; Verwey, 1995, 2003), designed to account for the unique characteristics of specific movement classes and the associated demands on memory and control mechanisms resulting from linkages among individual movement elements (Abrahamse, Ruitenberg, de Kleine, and Verwey, 2013). In examining the nature of lateral specialization of the two hemispheres for sequence learning, one can pose the question of whether lateralization of the hemispheres is specialized a.) for the motor output performance of the task, or b.) for the memory of the presented stimuli to perform the sequence, or c.) for both (see also Jason, 1983). One assumption is that very early in the sequence learning process, responses are dependent on the stimulus indicating the next element in the sequence, but with increasing practice response execution becomes more automatic such that one segment of the sequence triggers the next segment in the sequence (see Abrahamse et al., 2013; Hoffmann and Koch, 1997; Klapp and Jagacinski, 2011; Zirngibl and Koch, 2002). Therefore, one conclusion was that the stimuli that triggered the next segment of the sequence is somehow associated or tied to specific motor or visual-spatial information (see Deroost and Soetens, 2006; Shea et al., 2016). This idea is consistent with other theories of sequence learning which proposed a shift from external stimulus-based control to internal motor programs (Keele et al., 1995; Verwey, Shea, and Wright, 2015).

The primary purpose of the present experiments was to continue the process of systematically studying hemisphere specialization in sequence learning. More specifically, in contrast to the Ellenbuenger et al. (2012), and Schmitz et al. (2013) experiments, where visual information about the sequence was presented in different VHFs during sequence acquisition to investigate the formation of a sequence representation in the two hemispheres, in the current two experiments the focus was on the time required to recognize the stimulus to trigger an acquired movement sequence using the VHF paradigm. This was

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