NONDOMINANT-TO-DOMINANT HAND INTERFERENCE IN BIMANUAL MOVEMENTS IS FACILITATED BY GRADUAL VISUOMOTOR PERTURBATION

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Abstract-In simultaneous bimanual movements, interference between the hands is always a possibility, particularly when movements are spatially incongruent. In a previous study using bimanual target-directed movements and abrupt visual feedback perturbation of one hand, I showed asymmetric interference from the dominant to the nondominant hand. The signature of that interference reflected the directional control strength of the dominant hand, supporting a recent theory of functional lateralization of arm movements, and extending it to a bimanual context. Nondominant-to-dominant interference was not observed in this task. The current study in healthy young adults used a bimanual paradigm in which one hand had to adapt to a gradual visuomotor perturbation, while the other hand operated under kinesthetic control, without visual feedback. In this arrangement, the kinesthetically guided hand provides a canvas on which the visually guided, and perturbed hand can 'paint' its interference. Results of this study showed two patterns of interference: in some participants the nonvisible hand deviated in the same direction (isodirectional) relative to the perturbed hand, in others it mirrored the direction (anisodirectional) of the perturbed hand. In isodirectional participants, dominant-to-nondominant and nondominantto-dominant hand interference was symmetrical and relatively weak, whereas there was strong nondominant-todominant hand interference in anisodirectional participants, suggesting interference in the form of endpoint accuracy control strength of the nondominant hand. Based on these findings, the study discusses potential mechanisms enabling the nondominant hand to exert this control strength onto the dominant hand. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: motor adaptation, lateralization, direction control, endpoint control, upper limb, movement kinematics.

INTRODUCTION

Moving both arms simultaneously introduces the possibility of interaction between the movements. For repetitive, cyclical movements which are at the basis of the vast majority of studies on bimanual coordination, there is a well documented preference for mirrorsymmetric (in-phase) movements, which are easier to perform and are more stable compared to asymmetric (anti-phase) movements (Kelso, 1984; Carson et al., 1997; Swinnen, 2002). 'Everyday-movements' are typically more goal-directed, and often visually guided. There, the sensorimotor system needs to integrate visual and proprioceptive signals, providing information about target position through visual input, and about the current effector state through visual and/or proprioceptive input. This mapping between sensory and motor space can be conceptualized as internal representation of movement kinematics and dynamics (Shadmehr and Mussa-Ivaldi, 1994; Imamizu et al., 1998), and enables the system to compute the forward or inverse kinematics/dynamics of the controlled effector. These representations are adaptive: when movement dynamics or kinematics are altered, for example by introducing force fields (Shadmehr and Mussa-Ivaldi, 1994) or visual feedback perturbations (Roby-Brami and Burnod, 1995; Bock et al., 2003), the mapping gets updated through practice, so that movement plans reflect the changed sensorimotor relationship. In a bimanual context, manipulating the sensorimotor mapping of one effector introduces a potential for interference between the perturbed and the unperturbed hand. This, however, depends on the nature of the perturbation: In a bimanual task where one hand was perturbed through a force field to which it adapted, movement trajectories of the other, unperturbed hand were not affected (Diedrichsen, 2007). A recent study using an abrupt (i.e., with sudden onset) kinematic perturbation in one hand, while not providing visual feedback of the other hand, found directional interference between the hands (Kagerer, 2015). In this task, the interference was asymmetrical: as the dominant (right) hand adapted to the visual feedback perturbation, the nondominant (and nonvisible) left hand in most participants started to deviate in the same direction. When the left hand adapted to the perturbation, effects on the (nonvisible) right hand were negligible. Demonstrating that in concurrent bimanual movements the dominant hand causes interference by 'pushing' its own control strength onto the nondominant

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Abbreviations: dPMC, dorsal premotor cortex; EPX, lateral endpoint error; IDE, initial directional error; LQ, laterality quotient; M1, primary motor cortex; RMSE, root mean squared error.

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hand extends the dynamic-dominance hypothesis beyond its unimanual context. The hypothesis postulates that one feature that distinguishes the dominant from the nondominant arm is the efficiency with which the dominant arm controls limb segmental dynamics, and with that, directional control (Sainburg, 2002). The nondominant arm has been shown to be more efficient with load compensation, resulting in better endpoint accuracy (Bagesteiro and Sainburg, 2003). This is supported by studies in stroke patients with right hemisphere damage, whose ability to accurately control final position accuracy in arm reaches is compromised (Schaefer et al., 2007). It should be noted that the abrupt perturbation findings were different from a previous study that had used a sequential bimanual design (one hand first, then the other hand). That study had shown that opposite arm training improved the control strength of the subsequently trained contralateral arm: the nondominant left arm benefitted in terms of final position accuracy from right hand training, and the dominant right hand benefitted in terms of initial direction after left hand training (Sainburg and Wang, 2002).

In summary, the control strengths of each effector interact differently with its counterpart, depending on whether the interaction is simultaneous or sequential. This suggests fundamentally different processes for transfer vs. interference. In the context of transfer tasks, memory effects cannot be ruled out (Krakauer et al., 2005; Wang and Sainburg, 2006); the bimanual simultaneous approach avoids this.

Interestingly, the previous abrupt perturbation study (Kagerer, 2015) did not find nondominant-to-dominant hand interference. Since nondominant arm performance tends to be more variable than dominant arm performance, and control characteristics are not expressed as strongly, I argued that the abrupt perturbation and the resulting adaptation process might have attenuated the left hand's directional control system, for example by preventing it to switch to its impedance control mode early enough in the movement. Such a mechanism has recently been proposed in a model postulating a hybrid controller which regulates predictive and impedance control differentially depending on which arm is used (Yaday and Sainburg, 2011). Another contributing factor could be prefrontal inhibition that has been shown during adaptation to abrupt visuomotor perturbation (Gentili et al., 2013). I hypothesized that if there was nondominant-todominant hand interference during concurrent bimanual movements, it was more likely to occur when conditions were more conducive to bringing out the left hand's endpoint accuracy control strength.

The present study uses a gradual visuomotor perturbation, i.e., a perturbation that introduced a sensorimotor discrepancy in a series of small steps. This has previously been shown to make adaptation more efficient (Kagerer et al., 1997; Michel et al., 2007), possibly by down-weighting the initial directional control demands, and up-weighting feedback processing. If the (perturbed) left hand under these conditions interfered with the (nonvisible) right hand, one would predict that the interference would emerge in later phases of the movement, reflecting feedback processes. It would also suggest that in concurrent bimanual movements the direction of interference (reflecting hemisphere-specialized control mechanisms) depends on task parameters that favor the control strength of the adapting hand.

EXPERIMENTAL PROCEDURES

Participants

Thirty-four adults with a mean age of 20.9 ± 1.3 years were pseudo-randomly assigned to one of two groups of 17 participants; there were ten females in group 1, and nine in group 2. All participants were right-handed, as determined by their laterality quotient (LQ) obtained through the Edinburg Handedness Inventory (Oldfield, 1971); the mean LQ was 76.0 \pm 20.9. The Institutional Review Board at Michigan State University approved all experimental procedures.

Apparatus and procedure

Participants sat at a table with two joysticks (Thrustmaster® T16.000 M) on it side by side, and a 19" LCD widescreen monitor positioned horizontally above the joysticks preventing vision of the hands. Each joystick controlled a cursor whose position on the computer screen was displayed directly above the actual joystick position. The (x/y) time series was sampled at 75 Hz, using Presentation® software (Neurobehavioral Systems) for stimulus presentation and data acquisition.

Participants used the joysticks to move the two respective cursors simultaneously from two starting positions, 16 cm apart, to two targets (diameter: 1 cm) appearing either straight forward (90°) from its respective starting position, or straight backward (270°); movement amplitude was 7.5 cm, and target order was pseudorandomized. See Fig. 1 for stimulus display and experimental design.

Participants started with a visual baseline ('preexposure', 12 trials, six/target) during which they received online visual feedback for both hands in the form of the movement path displayed on the monitor. Participants had to hit both targets, remain in them for 500 ms until they disappeared, and then move back to the respective home positions. This was followed by a kinesthetic pre-exposure (12 trials, six/target) during which one hand (depending on the group the participant was in) did not receive visual feedback of the movement path and had to rely predominantly on kinesthetic information; home position and targets were displayed. In group 1, the right hand cursor remained visible, and the left hand operated under kinesthetic conditions, and in group 2 the left hand remained visible, and the right hand did not receive vision. Following this, both hands received visual feedback again for two trials, in order to allow the kinesthetically guided hand to recalibrate, before the movement trace disappeared again for that hand; these two trials were not further analyzed. After this, visual feedback for the hand that received it was rotated by 10° for every 20 trials, upto a maximum of 60° ('exposure'). For the right hand, the rotation was

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