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The impact of concurrent visual feedback on coding of on-line and pre-planned movement sequences

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ABSTRACT

The purpose of this study was to determine the extent to which participants could effectively switch from on-line (OL) to pre-planned (PP) control (or vice versa) depending on previous practice conditions and whether concurrent visual feedback was available during transfer testing. The task was to reproduce a 2000 ms spatial–temporal pattern of a sequence of elbow flexions and extensions. Participants were randomly assigned to one of two practice conditions termed OL or PP. In the OL condition the criterion waveform and the cursor were provided during movement production while this information was withheld during movement production for the PP condition. A retention test and two effector transfer tests were administered to half of the participants in each acquisition conditions under OL conditions and the other half under PP conditions. The mirror effector transfer test required the same pattern of muscle activation and limb joint angles as required during acquisition. The non-mirror transfer test required movements to the same visual–spatial locations as experienced during acquisition. The results indicated that when visual information was available during the transfer tests performers could switch from PP to OL. When visual information was withdrawn, they shifted from the OL to the PP-control mode. This finding suggests that performers adopt a mode of control consistent with the feedback conditions provided during testing.

1. Introduction

How movement sequences are represented, and processed in the brain, and which neural bases are associated during the course of learning have stimulated the research since Lashley's (1951) seminal work on 'The problem of serial order in behavior' (Bapi, Miyapuram, Graydon, & Doya, 2006; Hikosaka, Nakamura, Sakai, & Nakahara, 2002; Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Kirsch & Kunde, 2012; Korman, Raz, Flash, & Karnim, 2003; Nakahara, Doya, & Hikosaka, 2001; Shea & Kovacs, 2013; Shea & Wright, 2012; Tanaka & Watanabe, 2014). Theoretical frameworks of sequence learning have suggested that independent codes, coordinate systems or representations are responsible for sequence production and that several sources of information available during the course of practice assist the learning process (Keele et al., 2003). Further, these frameworks often argue that practice related changes occur. That is, the development of and the reliance on a particular representation changes during the course of practice depending on the practice conditions (Bapi et al., 2006; Dirnberger & Novak-Knollmueller, 2013).

One theoretical model by Hikosaka which is based on behavioral and brain imaging data (Bapi, Doya, & Harner, 2000; Hikosaka et al., 1999, 2002) proposed that the learning of movement sequences involves both a fast developing, effector independent component represented in a visual–spatial coordinate system (e.g., spatial locations of the end effector and/or sequential target positions), and a slower developing effector dependent component represented in motor coordinates (e.g., sequence of activation patterns of the agonist/antagonist muscles and/or achieved joint angles). Note that both coordinate systems are thought to develop in parallel and representations in both coordinate systems are learned concurrently, but each of the processes operates in a single coordinate system. Hikosaka et al. (1999) suggested that the representation for a given sequence is distributed in the brain in different forms (visual–spatial and motor) with distinct neural networks supporting sequence production. In an initial pre-learning stage in which participants perform actions in a discrete, step-by-step manner by relying on the sensorimotor transformation for each action, where sequence production relies on serial sensorimotor processes for each action. By repeating the actions in a fixed order, new connections are formed between the mechanisms for individual actions, thus enabling the participants to perform the actions sequentially without relying on these step by step sensorimotor processes. At this stage of practice sequence production relies primarily on visual–spatial coordinates, but with increasing practice there is a shift in the reliance to the motor

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coordinate system which is thought to be predominantly responsible for sequence execution later in practice (see also Bapi et al., 2000; Sakai et al., 1998).

Recent behavioral studies using an inter-manual transfer design have provided empirical evidence that not only practice, but other factors play an important role in determining the more effective coordinate system available for sequence production (Keele, Jennings, Jones, Caulton, & Cohen, 1995; Kovacs, Han, & Shea, 2009; Kovacs, Muehlbauer, & Shea, 2009; Park & Shea, 2005; Shea, Kovacs, & Panzer, 2011 for an overview, Verwey & Clegg, 2005). It appears that task complexity (number of reversal in the sequence and/or sequence duration), and the availability of concurrent visual feedback during sequence production play an important role in determining which of the two representations is the more effective coding scheme for sequence production (Panzer, Krueger, Muehlbauer, Kovacs, & Shea, 2009; Shea et al., 2011). Kovacs, Han, and Shea (2009), for example, had participants practice either a relatively simple or a slightly more complex sequence of extension flexion movements for 99 trials during one practice session. The simple sequence involved 3 movement reversals and the movement duration was 1300 ms, while the more complex sequence involved five reversals and the movement duration was 2000 ms. It is important to note that both movement sequences were constructed by summing two sine-waves such that the first 1300 ms of the longer sequence was the same as the shorter sequence. The amplitudes of the two sine-waves were 45° for the first and 30° for the second. Following 99 practice trials with a right limb a delayed retention and two effector transfer tests (left limb) were administered. In one transfer test, the target locations were a mirror image (mirror transfer test) and required participants to perform the same pattern of muscle activation and limb joint angles as required during acquisition with the contralateral unpracticed effectors. The second transfer test (non-mirror transfer test) required movements to the same visual–spatial locations experienced during acquisition, however, because the contralateral limb was used new un-practiced patterns of muscle activation and joint angles were required to achieve the target locations.

The results of the Kovacs, Han, and Shea (2009) experiment indicated that after 99 trials of practice the participants performance of the more complex sequence on the non-mirror transfer test, where the visual–spatial coordinates had been reinstated, was superior to performance on the mirror transfer test. Alternatively, mirror transfer performance of the simple sequence, which required fewer reversals, was superior compared to the non-mirror transfer. This later finding suggests that the simple sequence was more effectively coded in motor coordinates, which requires the same pattern of homologous muscle activation with the contra-lateral unpracticed limb, at this stage of practice. Indeed, the analysis of the kinematics for the simple sequences was consistent with those typically found for pre-planned movements (no on-line corrections) and the kinematics of the more complex sequence was consistent with on-line (feedback) control. That is, the kinematics of the more complex sequence with five reversals and duration of 2000 ms indicated that performers made iterative feedback based corrections during the progress of the movement, typically found in on-line controlled movements while the simple movement sequence was void of these types of corrections. This caused Kovacs and colleagues to hypothesize that the coordinate system used to code sequence information may be dependent on the control process used rather than the amount of practice or the sequence characteristics per se (Kovacs, Muehlbauer, & Shea, 2009; Verwey & Wright, 2004).

Another assumption related to control processes is that visual feedback is used for on-line control (Elliott, Helsen, & Chua, 2001; Glover, 2004; Woodworth, 1899). To examine the relationships between the visual–spatial coordinate system, on-line control, and the contribution of concurrent visual feedback Kovacs, Boyle, Gruetzmacher, and Shea (2010) had participants perform a complex sequence with five reversals under two acquisition conditions. In one acquisition condition participants were provided before and during the movement a template indicating the goal pattern and a cursor indicating the current position of their movement in an attempt to promote on-line control. In another condition the goal movement template was presented before responding but the template and cursor disappeared as soon as the movement began. This condition was designed to encourage participants to pre-plan the movement because extrinsic visual information was not available during response execution making on-line detection and correction of errors difficult. The results of this experiment provided clear evidence that participants in the on-line condition, where the template and cursor indicating the progress of the movement were available during movement execution, coded the sequence more effectively in visual–spatial coordinates. Participants in the pre-plan condition, where the template or cursor was not available during movement execution, coded the sequence more effectively in motor coordinates.

These results led the researchers to conclude that the coding of movement sequences is at least to some extent dependent on the external information available during sequence production (concurrent visual feedback) and the different control processes (pre-planning/on-line control) used to produce the sequence. It is also interesting to note that pre-planning and on-line control of movement sequences have been shown to utilize different informations and rely on different neural pathways. Furthermore, pre-planning determines the initial kinematic characteristics of the movement including timing and velocity, while the on-line control monitors and occasionally adjusts movement progress “in flight” but these adjustments are limited to the spatial characteristics of the sequence (Glover, 2004). In other words, shorter duration movements with few elements rely predominantly on pre-planning while longer duration movements with more elements have an initial pre-planned component after which movement control is gradually taken over by the on-line control mechanism.

Research on the development of the two coordinate systems and the shift in the reliance for sequence production is pre-dominantly aimed at practice (Bapi et al., 2000; Hikosaka, Rand, Miyachi, & Miyashita, 1995; Kovacs, Han, & Shea, 2009) and, to a lesser extent, on information provided during response production. A related but yet unresolved question is whether or not participants can effectively switch between coding schemes and modes of control depending on the information provided. This question is of theoretical interest for two reasons. First, the Hikosaka et al. (1999) 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 (Sakai et al., 1998). In line with the theoretical framework of the ‘parallel neural network model’ (see Hikosaka et al., 1999), it also seems possible that either coordinate system can be accessed in any specific sequence production situation (see Kurata & Hoshi, 2002; Kurata & Wise, 1988). Thus, depending on the available extrinsic information, performers use the most salient code for sequence production independent of the stage of practice (see also Clegg, DiGirolamo, & Keele, 1998; Kovacs, Han, & Shea, 2009). This view supports the theoretical idea of more parallel processing in movement sequence learning, where the two coordinate systems cooperate with each other for sequence production. In addition this research question has the potential to shed some light on the ongoing theoretical debate that the two coordinate systems represent two different kinds of representations that form the ends of a continuum and not dichotomous states (Keele et al., 2003; see also Abrahmase, Ruitenberg, de Kleine, & Verwey, 2013).

Second, an additional assumption of the planning–control model proposed by Glover (2004) is that participants can alternate between control modes on successive sequence productions, but attempt to choose the optimal control scheme given the nature of the sequence and characteristics of the performance environment. The view that pre-planning and on-line control complement one another was also developed by Woodworth (1899). The control of a movement was conceptualized as preprogrammed at the initial phase and corrected with visual feedback as the movement progressed, what Woodworth called