Impact of instruction on the acquisition of sequence knowledge in a sensorimotor task

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ABSTRACT

We examined whether and to what extent a sequence of finger movements can be learned and transferred to the untrained hand according to the muscle homology depending on the relative salience of response locations and effectors. Participants performed a discrete sequence production task, in which they were asked to learn a sequence of either key locations or of finger movements. Each training block was followed by a transfer block in which responding with the opposite hand was required. Before the last transfer block participants received an unexpected instruction. They had to reproduce the sequence of key locations instead of the sequence of finger movements and conversely, the sequence of finger movements instead of the sequence of key locations. The results do not support the existence of a sequence representation for the order of finger movements irrespective of the hand used.

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1. Introduction

Learning of sequence structures embedded in successions of external and internal events is fundamental to human cognitive ability. In the last two decades, a considerable number of studies have been conducted with the objective of understanding the mechanisms underlying the acquisition of sequence knowledge. One of the most frequently used paradigms is the serial reaction time (SRT) task (Nissen & Bullemer, 1987), in which participants respond to successively presented stimuli as quickly as possible usually by pressing response keys. In this task, the learned sequences have been shown to be easily transferable to other effectors indicating that the acquired sequence knowledge is largely effector-unspecific (e.g., Cohen, Ivry, & Keele, 1990; Grafton, Hazeltine, & Ivry, 2002; Keele, Jennings, Jones, Caulton, & Cohen, 1995; Willingham, Wells, Farrell, & Stemwedel, 2000). However, several studies have also demonstrated that sequence learning may involve an additional more effector-specific component (e.g., Bapi, Doya, & Harner, 2000; Berner & Hoffmann, 2008, 2009a, b; Deroost, Zeeuws, & Soetens, 2006; Panzer, Krueger, Muehlbauer, Kovacs, & Shea, 2009; Park & Shea, 2003; Richard, Clegg, & Seger, 2009; Verwey & Clegg, 2005). This type of

learning is often assumed to be related to motor coordinates of involved effectors, such as to adjustments of motor control to the biomechanical interactions between the fingers of one hand (e.g., Hikosaka, Nakamura, Sakai, & Nakahara, 2002; Verwey & Clegg, 2005; Verwey & Wright, 2004).

In order to distinguish between effector-specific (motor) vs. effector-unspecific (spatial) learning the paradigm of intermanual transfer has been used (e.g., Cohen, Pascual-Leone, Press, & Robertson, 2005; Deroost et al., 2006; Kirsch & Hoffmann, 2010; Kovacs, Han, & Shea, 2009; Kovacs, Boyle, Grutmatcher, & Shea, 2010; Panzer, Krueger, et al., 2009; Romei, Thut, Ramos-Estebanez, & Pascual-Leone, 2009; Witt, Margraf, Bieber, Born, & Deuschl, 2010). After training a repeating sequence with one hand subjects have to perform the sequence with the opposite hand. In one condition (parallel), responses are made to the original sequence of stimuli. Thus, the sequence of external events remains unchanged while a new unpracticed pattern of muscle activation and joint angles is used due to the effector change. Accordingly, measured performance can be assumed to capture effector-unspecific learning of stimuli and of response locations. In another condition (mirror), the original stimulus sequence is reversed around the vertical midline. As a result, participants' responses involve a sequence of movements homologous to those used during training. Since the motor coordinates are assumed to be reinstated here in contrast to the changed visual coordinates of response locations and stimuli, the performance can be assumed to be related to some aspects of motor (i.e. effector-specific) learning. According to this rationale sequence knowledge acquired with one hand can be

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stored and transferred to the opposite hand in a body-related frame of reference that takes into account the mirror symmetry of muscles and joints (e.g., Shea, Kovacs, & Panzer, 2011). For a task that requires movements of multiple fingers of both hands, e.g., this implies that a representation exists for the order of finger movements independent of the hand used. That is, executing movements mirroring previously learned may merely require the redirection of the original motor commands to the contralateral hand (e.g., Gordon, Casabona, & Soechting, 1994; Parasher, Roy, & Gordon, 2001). The issue of coactivation of homologues muscle groups has been extensively investigated in bimanual coordination tasks and the results of numerous studies appear to support the view that there is a level of motor control of homologues muscles that is more natural than the control of nonhomologues muscles (e.g., Kelso, 1984; Li, Levin, Forner-Cordero, Ronsse, & Swinnen, 2009; Swinnen, 2002; but see Mechsner, Kerzel, Knoblich, & Prinz, 2001 and Mechsner & Knoblich, 2004). Nevertheless, whether mirror transfer might reflect transfer of effector-specific knowledge in learning tasks, in which homologues muscles of two effectors are not simultaneously activated, is a matter of a debate (cf. Grafton et al., 2002; Verwey & Clegg, 2005). Accordingly, one purpose of the present experiment was to test whether and to what extent a succession of finger movements can be learned and transferred from one hand to the other in motor coordinates.

Another potentially important factor has not received much attention in the discussion of effector-specific learning so far. In many sequence learning tasks subjects are instructed to *press keys* in response to *stimuli*. Thus, stimuli and response locations (i.e. keys) are emphasized by instruction. Accordingly, a dominance of effector-unspecific knowledge typically observed in SRT tasks may be a result of the experimental setting, in which stimuli and response locations are more attended than effector movements. Some results from studies using extension-flexion arm movements, which report a prevalence of motor knowledge following relatively short practice, appear to support this possibility (e.g., Panzer, Krueger, et al., 2009). In these studies effector movements have to be attended at least as much as external stimuli to perform the task successfully. The crucial role of selective attention, or more generally, of a particular task set has also been recognized in a recent review of SRT literature (Abrahamse, Jiménez, Verwey, & Clegg, 2010). The authors argue that a main determinant of a formed representation is a set of cognitive processes including a processing goal, detailed specifications of stimulus and response features and their mapping, all of which are highly sensitive to given task characteristics.

Against this background we aimed to implement optimal conditions for effector-specific learning and transfer. For this purpose one group of participants (henceforth finger group) performed a version of the discrete sequence production task (DSP) previously applied by Verwey and colleagues ([1], e.g., Verwey, 1999; De Kleine & Verwey, 2009) in which they were asked to practice a succession of finger movements by pressing a sequence of keys. In order to eliminate any influence of stimulus sequences the subjects were required to memorize the sequence so that it could be reproduced from memory in response to an imperative cue. Moreover, each regular training block was followed by a transfer block in which a response with the opposite hand according to the instruction, was required. That is, participants were required to reproduce the learned sequence of finger movements with homologous fingers of the transfer hand. This corresponds to mirror conditions applied in previous studies. By mean of this procedure participants were virtually forced to learn an effector sequence. After extensive training a test block with an unexpected transfer instruction was introduced.

Participants were now asked to reproduce the sequence of key locations instead of the sequence of finger movements.

The performance of the finger group was contrasted with the performance of another group of participants (henceforth key group), who practiced a sequence of key locations corresponding to the sequence of finger movements practiced in the finger group. That is, apart from the instruction, participants performed the same task in both groups during practice. As in the finger group, each practice block was followed by a transfer block, in which responding with the opposite hand was required. However, according to the instruction the task was to transfer the sequence of key locations instead of finger movements now, what corresponded to the parallel transfer conditions previously used. Moreover, in the last test block participants were asked to reproduce the sequence of finger movements instead of the sequence of key locations.

Previous research with the DSP suggested that discrete keying sequences can be represented by one or more motor units, or "chunks", which may rapidly be selected and executed as a whole (e.g., Verwey, 1999; 2001; cf. also Kirsch, Sebald, & Hoffmann, 2010; Koch & Hoffmann, 2000). The issue of how motor chunks are being coded has been investigated in several studies and there is evidence that effector-specific learning may thereby play a role (De Kleine & Verwey, 2009; Verwey & Wright, 2004). Thus, the implemented version of the DSP appeared to be well suitable to study effector-specific learning and allowed us to test three predictions: (1) If a sequence of finger movements can be learned and transferred to the opposite hand in motor coordinates irrespective of the original instruction, then the performance in the finger group would involve learning a single sequence in practice and transfer blocks, while the performance in the key group should involve learning two sequences of finger movements, one in the practice and one in the transfer blocks. Moreover, limited transfer of knowledge to the unexpected block can be expected for the finger group, whereas considerable transfer should occur in the key group. (2) If a sequence of key locations is learned in both instruction conditions, then an opposite pattern of results should emerge. That is, in the finger group two sequences of key locations should be learned during the practice and transfer blocks and a considerable transfer to the unexpected block can be expected. In the key group, in contrast, one sequence should be learned and limited transfer to the unexpected block should be observed. (3) If, however, the acquired sequence knowledge really refers to what had been originally instructed then one sequence of finger movements should be learned and transferred in the finger group. Analogously, one and the same sequence of key locations should be accessed during learning and transfer blocks in the key group. Moreover, performance in the last transfer block including an unexpected instruction should likewise be deteriorated in both groups. That is, if subjects had indeed learned a sequence of finger movements, they should be impaired in reproduction of the sequence of key locations because the learned sequence of finger movements is changed by this manipulation. Conversely, if subjects had indeed learned a sequence of key locations, performance should similarly decrease for the reproduction of the sequence of finger movements because the learned sequence of key locations is changed by this manipulation.

The mentioned pattern of results supporting the first hypothesis would suggest that learning of a sequence of finger movements (i.e. effector-specific motor learning) may develop independently of strategic influences (cf. e.g., Hikosaka et al., 2002) and thus, would emphasize the impact of effector-specific learning in sensorimotor sequence learning tasks. If the second prediction would be confirmed by the results, then the proposal of Willingham and colleagues (e.g., Willingham et al., 2000) will be strengthened suggesting a dominant role of effector-unspecific learning of response locations in SRT like tasks. This pattern, however, can also be expected if potentially acquired effector-specific knowledge is not transferable to the opposite hand. The third prediction is in line with a view that distinct learning mechanisms may differently be involved depending on the nature of the task (e.g., Abrahamse et al., 2010).

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[1] In this task participants typically practice movement sequences of limited length by responding to fixed series of key specific stimuli. In contrast to SRT task, in which a sequence is continuously repeated, discrete sequences in the DSP task are separated in time by a pre-cue signaling the begin of a sequence.
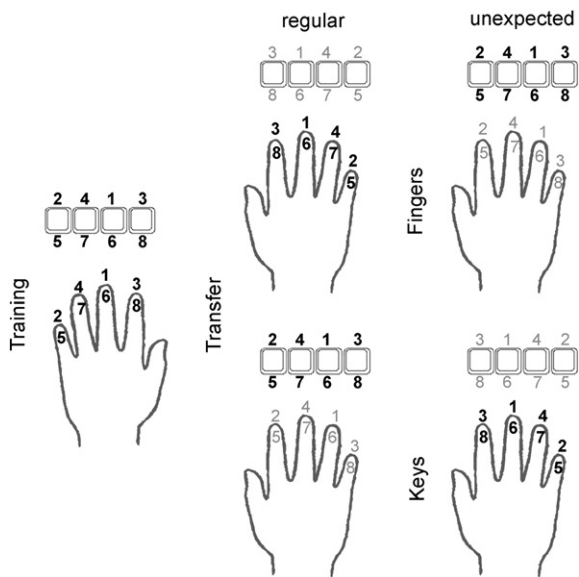
Fig. 1. <u>Left</u>: The learned response sequence as presented in the finger (bottom) and in the key (top) conditions during the first acquisition block as well as during other blocks when participants committed errors. Digits represent the order of to be pressed keys and the corresponding sequence of the fingers of the left hand by which the keys are to be pressed. Digits illustrated at the top of the hand and of the keys reflect the first half of the sequence, while the lower digits stand for the second half of the sequence. That is, the succession of fingers was: middle finger (1), little finger (2), index finger (3), ring finger (4), little finger (5), middle finger (6), ring finger (7) and index finger (8). <u>Middle</u>: schematic representation of the movement sequences required in the regular transfer blocks in the finger and key conditions. <u>Right</u>: to be performed sequences during the test block with an unexpected instruction. Note: digits representing the same sequence of fingers and of keys among experimental conditions are shown in black.

2. Method

2.1. Participants

Twenty-eight undergraduate students of the University of Wuerzburg participated in partial fulfilment of course requirements. They gave their informed consent for the procedures. The sample comprised twenty-three females and five males, with ages ranging from 19 to 30 years (mean age 21.5, $SD = 2.9$). All of them reported to be predominantly right-handed (i.e. they reported for each of the succeeding tasks to typically perform it with their right hand: painting/drawing, throwing a ball at a target, using an eraser, dealing cards with the hand not holding the deck).

2.2. Task and apparatus

The keys G, H, J and K on a standard (German) QWERTZ keyboard served as response keys. These keys were marked in order to make them more salient and to prevent the vision of the alphabetic characters. When the right hand was used for responding, the keys were assigned from left to right to the index, middle, ring and little fingers respectively. For the left hand, the assignment was inverted (i.e. the left-most key had to be pressed with the little finger etc.). Participants were asked to produce a sequence of eight key presses as fast and accurately as possible in response to an acoustic go signal (a short beep sound). One second before the imperative signal occurred, another acoustic warning cue was presented (the German word for "attention"). After each trial, participants initiated the next trial by pressing the space-bar on the keyboard.

2.3. Experimental procedure and design

The experiment consisted of 19 blocks of trials. There were four types of blocks: an acquisition block (AQ), 9 practice blocks (PR), 8 transfer blocks (TR) and a test block (TE). The succession of these blocks was AQ(1), PR(2), TR(3), PR(4), TR(5), PR(6), TR(7), PR(8), TR(9), PR(10), TR(11), PR(12), TR(13), PR(14), TR(15), PR(16), TR(17), PR(18), TE(19). AQ and PR were performed with the left hand and TR and TE were performed with the right hand.

The first block was an acquisition block, which was not considered in the analyses. During this block, participants were asked to learn either a sequence of key locations or a sequence of finger movements by pressing response keys with their left hand. In this block, an image of a hand or of four keys was shown together with digits indicating the succession of responses (see Fig. 1, left). Participants were instructed to memorize the respective sequence so that it could be reproduced from memory in the succeeding blocks. The sequence illustrated in Fig. 1 (left) was repeated twenty times during the first block. This second-order conditional sequence consisted of eight elements and required successive pressing of the keys with middle (1), small (2), index (3), ring (4), small (5), middle (6), ring (7) and index (8) fingers. This sequence was used for both instruction conditions and for all subsequent practice blocks performed with the left hand.

The acquisition block was followed by a first practice block, in which an illustration of the required sequence was only shown if subjects committed errors. That is, subjects had to recall the succession of key locations or the succession of finger movements from memory. Beginning with this block, practice blocks alternated with transfer blocks, in which the same sequence of key presses or of finger movements had to be performed with the opposite (i.e., right) hand according to the instruction condition. Thus, subjects who were instructed to memorize a sequence of key locations were asked to reproduce the succession of the key locations learned. In contrast, in the finger condition, the reproduction of the learned sequence of finger movements was required (see Fig. 1, middle part). The number of trials was 20 for regular learning blocks and 5 for transfer blocks.
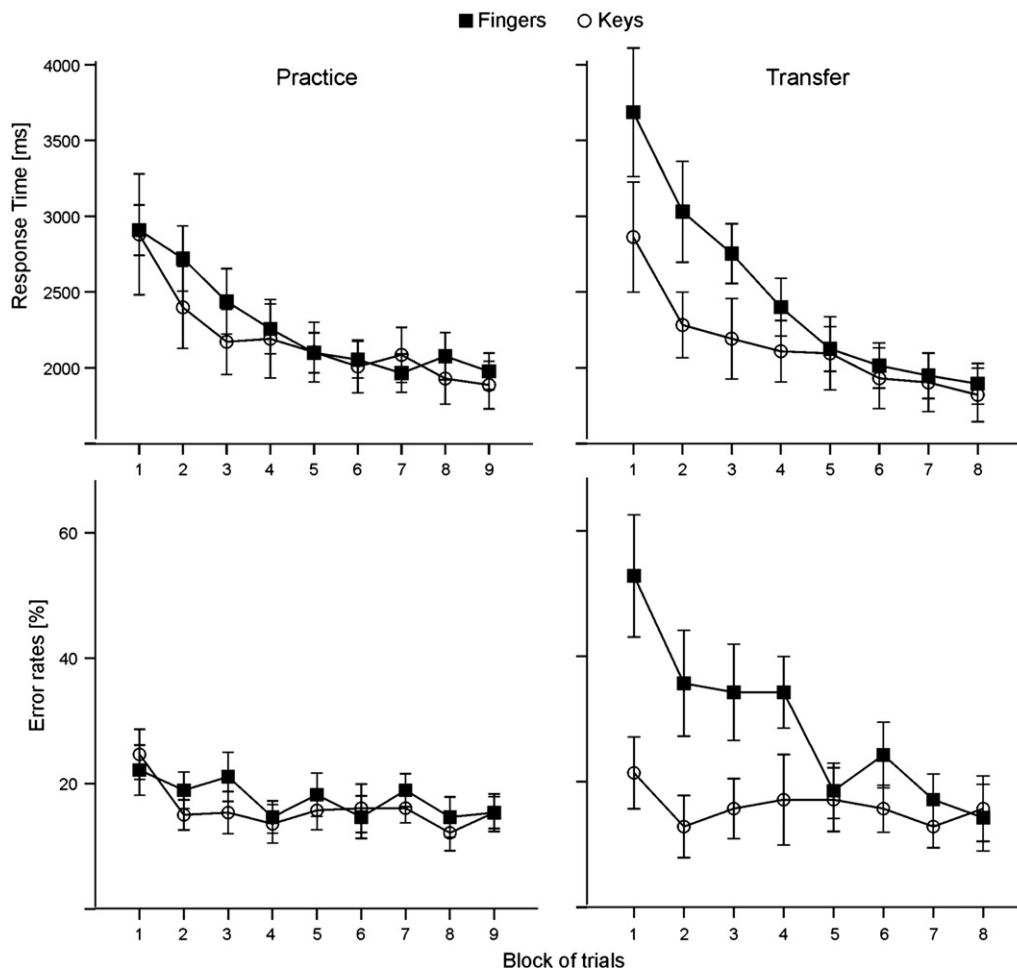
After nine practice and eight transfer blocks were performed (i.e. after the sequence was practiced 200 times with the left hand and 45 times with the right hand), an additional transfer block with an unexpected instruction was implemented. In this last test block subjects were asked to reproduce the sequence of finger movements, if they previously trained the sequence of key locations. And conversely, if they practiced the finger movement sequence before, they were then asked to reproduce the sequence of key locations (see Fig. 1, right). In this block, which contained 20 trials, responses were performed with the right hand as in all preceding transfer blocks. Thus, we used this last block as a test block, by means of which we aimed to access changes in intermanual transfer associated with the changed transfer instruction.

After a full sequence had been entered participants received feedback about whether their response was correct and if the response was correct, what their response time was. When a response was incorrect the original image of the sequence was shown until the next trial was initiated. Moreover, at the end of each block participants were informed as to their mean RTs and the number of errors and they were asked to optimize their performance (i.e. to accelerate the responding and to make fewer errors).

3. Results

3.1. Response times

The latency between the onset of the go-signal and the last key press was defined as response time (RT). RTs from correct trials were averaged for each block. Some subjects did not succeed in reproducing the response sequence during some transfer blocks or during the last

Fig. 2. Mean response times (top) and error rates (bottom) per block of trials for both instruction conditions separately for regular practice and transfer blocks. Note, each of the first eight regular practice blocks was followed by a regular transfer block. The last practice block was followed by a test block with unexpected instruction (not shown).

unexpected block. In these cases no response time data were available (1.5% of the averaged data). These missing values were excluded from the analyses of response times.[2]

The mean RTs for the regular practice and transfer blocks are shown in Fig. 2 (top). The average RTs of practice blocks decreased in the course of training for both conditions. These practice related changes in performance are substantiated by the results of an analysis of variance (ANOVA) with block as a within-subjects factor, and instruction as between subjects factor. This ANOVA revealed a significant main effect of block, $F(8, 208) = 30.50$, $p < .001$, partial $\eta^2 = .540$. We also computed RT differences between transfer blocks (3, 5, 7, 9, 11, 13, 15, 17) and practice blocks preceding these transfer blocks (2, 4, 6, 8, 10, 12, 14, 16; i.e. transfer costs). An ANOVA performed on these values with block and instruction as factors yielded significant main effects for instruction, $F(1, 22) = 14.04$, $p = .001$, partial $\eta^2 = .390$, and for block, $F(7, 154) = 5.19$, $p < .001$, partial $\eta^2 = .191$, and a significant interaction between both, $F(7, 154) = 3.73$, $p = .001$, partial $\eta^2 = .145$. This result indicates that transfer costs decreased at a higher rate for the finger than for the key condition being also generally higher for

the finger condition than for the key condition early during training (cf. Fig. 2). Since there were no differences between the instruction conditions during the regular practice blocks the result suggests that more learning took place in the finger than in the key condition during the transfer blocks. This pattern is most compatible with the assumption that in the finger condition two spatial sequences of key locations were learned during the practice and transfer blocks whereas one sequence of key locations was used during learning and transfer in the key condition.

In order to quantify the influence of the changed instruction implemented in the last test block, we computed RT differences between the last regular practice block (18) and the last regular transfer block (17) as well as between the last practice block (18) and the following test block (19), in which the original instruction has been changed. This analysis aimed at assessing the impact of the instruction on the acquired sequence representation: if under the finger instruction a sequence of finger movements is preferably learned and under the key instruction a sequence of key locations, the unexpected transfer to the respective other sequence should likewise be difficult to accomplish for both groups. If, however, one learning form dominates irrespective of the original instruction, the performance in the last test block should differ between both instruction conditions.

An analysis of variance (ANOVA) revealed a significant effect for the type of transfer, $F(1, 24) = 9.01$, $p = .006$, partial $\eta^2 = .273$, indicating that the costs were generally higher for a transfer to the respective other sequence than for the last regular transfer block, and a significant interaction between the type of transfer and the

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[2] Two subjects from the key condition were not able to transfer the learned sequence of key locations into a sequence of finger movements during the last test block. During some of the regular transfer blocks four subjects failed to transfer the learned sequence to the opposite hand (3×finger condition, 1×key condition). Thus, the analyses of regular transfer costs (see below) included 13 subjects from the key condition and 11 subjects from the finger condition. For the analyses of the last test block the data of 14 subjects from the finger condition and of 12 subjects from the key condition were available.

instruction condition, $F(1, 24) = 6.49$, $p = .018$, partial $\eta^2 = .213$. In the finger condition, the transfer to the sequence of key locations caused only marginal costs, whereas in the key condition, the transfer to the sequence of finger movements considerably decelerated RTs as compared with the preceding regular transfer block (see Fig. 3 (left) for means). Thus, the transfer from fingers to keys proved to be substantially easier than the transfer form keys to fingers. This result indicates that participants of the finger group possessed considerable knowledge about the spatial key locations, whereas participants of the key group could access the finger movement sequence to a much lesser degree. Accordingly, consistent with the data of the regular learning and transfer blocks, spatial learning appeared to dominate irrespective of the original instruction.

3.2. Errors

The analyses of the error rates revealed a pattern of results, which was highly comparable to that observed in the analyses of the response times. The mean error rates observed during regular practice and transfer blocks are shown in Fig. 2 (bottom). These values were analyzed in a manner analogous to the response times. The error rates of the regular practice blocks significantly decreased in the course of the experiment, $F(8, 208) = 4.29$, $p < .001$, partial $\eta^2 = .142$. The analysis of the transfer costs yielded significant main effects for factor block, $F(7, 182) = 2.42$, $p = .021$, partial $\eta^2 = .085$, and instruction, $F(1, 26) = 11.36$, $p = .002$, partial $\eta^2 = .304$, and a significant interaction of both, $F(7, 182) = 3.09$, $p = .004$, partial $\eta^2 = .106$. This interaction arose because transfer costs were absent when subjects practiced the sequence of key locations. For the finger condition in contrast, high transfer costs were evident at the beginning of the training and they decreased in the course of training (cf. Fig. 2).

Like the results of the response times, error rates considerably increased when the practiced sequence of key locations had to be transferred to the corresponding sequence of finger movements, whereas the transfer from the learned sequence of finger movements to the corresponding sequence of key locations caused only a marginal increase in error rates. However, an ANOVA including error costs of the last regular transfer block and the test block with changed instruction only revealed a significant main effect of transfer type, $F(1, 26) = 4.85$, $p = .037$, partial $\eta^2 = .157$. The main effect of instruction as well as the interaction between transfer type and instruction approximated but did not reach the significance threshold, $F(1, 26) = 3.39$, $p = .077$, partial $\eta^2 = .115$, and $F(1, 26) = 2.33$, $p = .139$, partial $\eta^2 = .082$. Fig. 3 (right) illustrates the according means.

Based on these results we examined the error costs of the transfer to the respective other sequence separately by testing the error-differences between the last practice block (18) and the test block (19) against zero. In the finger condition, there were no significant

error costs, $t(13) = .627$, $p = .541$. In contrast, in the key condition, a significant increase in error rates was observed, $t(13) = 2.57$, $p = .023$. Thus, only the transfer from the practiced sequence of key locations to the corresponding sequence of finger movements costs additional errors but not the transfer from the practiced sequence of finger movements to the corresponding sequence of key locations.

4. Discussion

We investigated the influence of different learning conditions on the representation acquired during a perceptual-motor task. In particular, we were primarily interested in whether and to what extent a sequence of finger movements can be learned and transferred to the untrained hand according to the muscle homology depending on the relative salience of the to be pressed keys and of fingers by which the keys are to be pressed. For this purpose we asked the participants to learn either a succession of key presses or a sequence of finger movements and by repeatedly testing learning performance with the opposite hand. Performance measured in the transfer blocks was assumed to be indicative of whether the sequence of key locations or of finger movements has been learned in both groups of participants. Three patterns of results were predicted: (1) Learning of finger movements irrespective of the instruction was assumed to be expressed in learning and transfer of a single sequence during regular blocks, and in a limited transfer to the unexpected block in the finger group. In the key group, two sequences of finger movements were expected to be learned during practice and transfer blocks, and a considerable transfer to the unexpected block could be assumed. (2) Learning of key locations in both groups, in contrast, should produce an opposite pattern of results: learning of two sequences, and considerable transfer in the last test block in the finger group, and learning of a single sequence and limited transfer in the last block in the key group. (3) Learning according to the instruction was assumed to be associated with learning and transfer of a single representation required by the instruction, and with a limited transfer to the last test block, in which the original instruction has been changed.

The observed results appear to provide strong support for the second hypothesis. The performance in the last unexpected test block deteriorated much more, when a sequence of response locations had been practiced and the corresponding sequence of finger movements had to be reproduced subsequently, as compared with the condition, in which a sequence of finger movements had been practiced and the reproduction of response locations was unexpectedly required. Response times and errors associated with transfer to the opposite hand considerably increased, when the original instruction was changed in the location condition. In contrast, in the finger condition, RT costs only marginally increased after the original instruction had been changed, while there were no significant error costs at all. Thus,
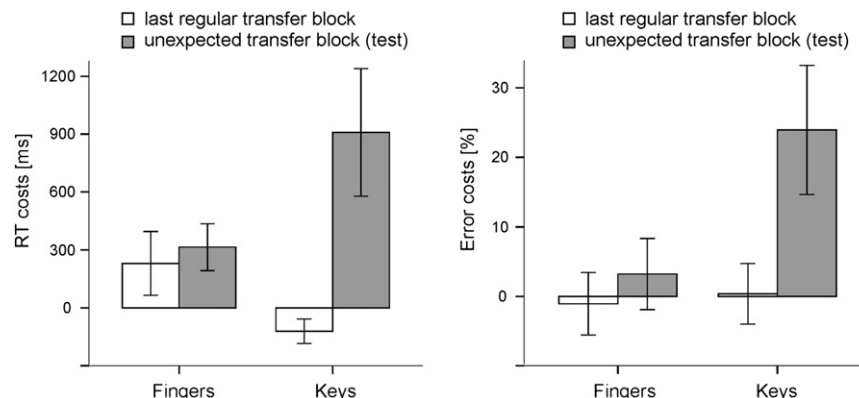

Fig. 3. Mean RT (left) and error costs (right) as a function of the transfer type and, finger and key conditions. Error bars are standard errors.

in spite of the instruction participants of the finger group seemed to learn the succession of key locations. In contrast, participants of the key group seemed to ignore the succession of finger movements.

Moreover, regular transfer costs were higher for the finger condition than for the key condition early during training but they were comparable for both conditions at the end of practice. The stronger decrease in transfer costs for the finger than for the key condition indicates that learning took place during transfer blocks in the finger condition (at least to a higher degree than in the key condition). This finding appears to fit well to the results of the last test block and speaks for that in the finger condition two sequences of key locations instead of one sequence of finger movements have been learned whereas a single representation was used for learning and transfer in the key condition. In other words, learning sequences of keys to be pressed instead of sequences of fingers to move, seem to prevail against the additional effort it costs to learn two instead of one sequence.

These results are consistent with the hypothesis of Willingham et al. (2000) suggesting that sequence knowledge acquired in SRT like tasks is dominated by knowledge related to the spatial locations of keys. A new and somewhat unexpected aspect of the present results is that we did not find indications of effector-specific learning and transfer even in the finger condition, in which effector-specific learning is stressed and explicitly required by task characteristics. Thus, the existence of a sequence representation in terms of finger movements that can be transferred between hands in motor coordinates does not appear to be supported by the results.

One possible reason for the observed dominance of effector-unspecific knowledge might be related to temporal constraints of the development of effector-specific knowledge. Results of several studies suggested that with extensive practice sensorimotor skills become increasingly effector-specific (e.g., Bapi et al., 2000; Hikosaka et al., 2002; Verwey & Clegg, 2005). According to Hikosaka et al. (2002), e.g., spatial and motor sequence learning processes operate in parallel, but contribute differently to the performance depending on the stage of practice. Spatial learning is assumed to dominate at the beginning of training, while motor knowledge is given more weight with practice. This approach might possibly explain why in the finger group participants obviously tended to learn two spatial sequences of key locations instead of a single sequence of finger movements. It should be noted, however, that the emergence of effector-specific sequence knowledge does not seem to depend exclusively on amount of practice. Panzer and colleagues (Panzer, Krueger, et al., 2009) e.g., demonstrated that movement sequences can be coded in motor coordinates more effectively than in visual-spatial coordinates relatively early in practice (i.e., following 99 sequence repetitions). Kovacs, Mühlbauer, & Shea (2009) in contrast, reported that following extensive practice of up to 12 days (including up to 1,920 sequence repetitions) the visual-spatial coordinates still dominated (cf. also Panzer, Muehlbauer et al., 2009). Thus, other task characteristics may be at least as important as the amount of practice. Nevertheless, even though the sequences were extensively practiced in the present study, the amount of training may not have been sufficient to enable motor learning.

The results might, however, also be considered as a hint that sequence knowledge is generally dominated by knowledge related to the distal effects of the sequence of movements, even if the task emphasizes the effectors. There are findings, e.g., suggesting that directing attention to effectors or to effector movements ("internal focus of attention") may result in less effective skill learning compared with conditions, in which attention is directed to the effects of movements ("external focus" of attention, see e.g., Wulf & Prinz, 2001; Wulf & Shea, 2002; Wulf, Shea, & Lewthwaite, 2010 for reviews). According to a constrained action hypothesis (Wulf, McNevin, & Shea, 2001) an internal focus on innate movements interferes with automatic motor control processes, which normally regulate the movement when movement outcome is focused. As suggested by Wulf & Prinz (2001), to direct attention to the anticipated effect of a movement might be more effective (and more "natural") than to focus on the details of the movement because distal action effects may enable commensurable coding of efferent and afferent information (i.e., of perception and action planning). Accordingly, effector-unspecific sequence learning may generally dominate over effector-specific learning due to its closer relation to a "natural" way of action planning and control.

The failure to find indications for learning of the finger movement sequence may also be due to the fact that the paradigm of intermanual transfer does not provide valid indicators of effector-specific learning. That is, participants might have acquired effector-specific knowledge in the present task, but it was not expressed in the performance of the implemented finger transfer blocks. One possible reason might be that effector-specific knowledge is not transferable at all (cf. e.g., Verwey & Clegg, 2005). As a result, participants may have attempted to solve the problem of the intermanual finger transfer in an external frame of reference rather than based on muscle homology (cf. e.g., Grafton et al., 2002; Verwey & Clegg, 2005), i.e., by transforming the sequence of key locations practiced with the left hand into a new sequence of key locations according to the original sequence of finger movements. Alternatively, effector-specific learning might also be "sensory" in nature (e.g., stimulus-based, cf. Berner & Hoffmann, 2008) and thus, only transferable in external rather than in motor coordinates. Accordingly, further research is needed to examine the usefulness of intermanual transfer paradigms for measuring of indicators of effector-specific learning.

In light of the evidence for diverse forms of sequence learning as well as for the influence of diverse task characteristics on the particular learning mode we consider the present experiment as an attempt to further refine the theoretical questions about the precise nature of the assumed representations and their possible interactions. Our results do not support the existence of a sequence representation for the order of finger movements irrespective of the hand used and thus, suggest that sequence knowledge acquired in sensorimotor tasks is dominated by knowledge related to the selection of spatial targets for movements even if effector-specific motor learning is required.

Acknowledgments

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