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Sequences in the discrete sequence production task are represented in a hand-based frame of reference

Eddy C. Groen (s0129518)

Faculty of Behavioral Sciences, University of Twente, the Netherlands

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Primary mentor: prof. dr. ing. Willem B. Verwey

Secondary mentors: dr. Elger L. Abrahamse, dr. Elian de Kleine

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Abstract

How come we are able to adapt to changes in our environment so well when performing tasks with both our hands? Twenty-four right-handed participants practiced 2 bimanual discrete sequence production (DSP) sequences with both hands placed adjacently. In 2 test phases (little vs. extensive practice), the right forearm was moved 90° outward. Performance was slowed ($p < .01$) and the hands did not differ in the amount of slowing, nor was this effect different after extensive practice (Fs < 1). It suggests that we use hand-based frames of reference that readjust by slowing all components of a sequence. Chunks containing keypresses by both hands and an equal slowing for both hands suggest that these frames may also overlap.

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Trained keyboardists are seemingly able to play an intricate piece of music just as easily on two separate keyboards as they do on a single keyboard. This holds true even if the keyboards vary strongly in relative position to one another. Avid gamers appear to have no difficulty placing and replacing their fingers closer to, and farther away from one another on a controller or a computer keyboard in order to move around a virtual world with great agility. How come such a trained order of movements can be separated in space with relative ease? What does this say about the way this kind of information is stored and retrieved in our memory?

In order to answer such questions, we must understand how the human brain encodes our movements. Keyboardists and gamers alike must have a sense of (a) where to place their fingers within the environment, (b) which fingers are to be used at a given time and which are not, and (c) how hard or how fast a key must be depressed. In other words, *action sequences* are series of motor actions in a fixed order, which contain both a spatial component that prescribes locations in three-dimensional space and a non-transferable motor component that regulates muscle movement (Hikosaka et al., 1999). This experiment set out to determine to what extent a spatial manipulation affects the execution of a sequence performed by two hands. To this end, participants practiced two 6-key bimanual *discrete sequence production* sequences (DSP sequences; see Rhodes, Bullock, Verwey, Averbeck, & Page, 2004, for a review) with both hands placed close to one another. Different from *serial response time* sequences (SRT sequences; Nissen & Bullemer, 1987), DSP sequences are discrete in having a clear-cut start and end, as well as a 0 ms response-cue interval, with the first cue becoming the imperative for the entire sequence after sufficient practice, so that the subsequent cues can even be completely omitted (cf. De Kleine & Verwey, 2009). After little practice and later after extensive practice, the right forearm was moved 90° to the right. This was expected to slow sequence execution, providing insight into the way our hands collaborate.

Every time we learn a new action sequence, the brain first maps spatial coordinates at a very abstract level (Witt, Ashe, & Willingham, 2008), allowing us to quickly learn new tasks and adequately performing sequences even with limited practice. At this point, the procedural knowledge is also available for other effectors (Witt et al., 2008), such as the other hand or a different configuration of fingers from the same hand (e.g., Verwey, Abrahamse, & Jiménez, 2009). Thus, sequence knowledge at this stage can be described as *effector-independent*. Following more extensive practice, learning occurs at both motor and spatial levels, allowing us to remain adaptive while sequential motor skills are refined and consolidated at the motor level by storing the order of individual events (Hikosaka et al., 1999; Verwey & Wright, 2004; see also Bapi, Doya & Harner, 2000; Verwey, 2003). This entails more direct control of the effectors involved, adapted to their respective abilities and limitations (Bapi et al., 2000; Berner & Hoffmann, 2008; Park & Shea, 2003; Verwey et al., 2009). In other words, through practice the sequence knowledge becomes *effector-specific* (Bapi et al., 2000; Park & Shea, 2003; sometimes also called effector-dependent), as the instructions for a specific effector no longer take the properties of other effectors into account. This makes transfer of sequence knowledge to other effectors much more difficult in terms of RT and accuracy (Berner & Hoffmann, 2009a) but allows more efficient execution by the designated effectors. So with practice, effector-specific components develop at the motor level.

As the brain shifts towards motor learning, the spatial component remains important. Grafton, Hazeltine, and Ivry (1998) found SRT sequences learned on a smaller keyboard can transfer well to a large keyboard with keys placed far apart, thereby requiring arm movements, which shows that spatial aspects of sequence execution can be encompassed, at least when limited to one hand. Using a DSP task, De Kleine and Verwey (2009) found that the performance on highly practiced DSP sequences decreases when the practiced hand performs the same sequence on a different location. This is in line with theories on a parallel dual-processor system, which hold that an effector-independent cognitive processor concatenates groups of actions into *motor chunks* (Verwey, 2001) and an effector-specific motor processor translates these chunks into spatial actions within a given *frame of reference* (Verwey, 2003). Motor chunks are smaller subsets of keypresses, which are necessary when learning and executing longer action sequences due to neural limitations (Verwey, 2001; Verwey, Lammens, & Van Honk, 2002). They allow for faster performance on action sequences than if effectors (i.e., fingers) were triggered individually (Proctor & Dutta, 1993; Witt et al., 2008). Chunks are thus necessary components for efficient production of longer action sequences and they include a location-specific component, using one or more frames of reference.

We continuously monitor and update the relative placement of ourselves and of objects in our environment by placing them in an allocentric or egocentric frame of reference. In an allocentric frame of reference, the object is stabilized to features of our environment, either in relation to the room, a geographic location or another object (Witt et al., 2008), while in an egocentric frame of reference, we consider the object an extension of ourselves (Maravita & Iriki, 2004; Mou, Biocca, Owen, Tang, Xiao, & Lim, 2004), relating its position and orientation to parts of the body, such as the head, eye, shoulder, forearm, hand, torso, or the entire body (Colby & Goldberg, 1999; Witt et al., 2008). Verwey and Wright (2004) assert that the formation of effector-specific components of sequential motor skills involves both an allocentric and an egocentric frame of reference. From the early stages of sequence learning on, a higher-level egocentric frame of reference represents the sequence, allowing the abstract sequence representation to easily be transferred to other effectors (Witt et al., 2008). In a DSP study, Verwey et al. (2009) found that performance on sequence production is slowed less with transfer to other fingers of the same hand than to fingers of the other hand, supporting the notion of an egocentric frame of reference. In an SRT study by Abrahamse, Van der Lubbe and Verwey (2007), sequence execution and mental representation formation were impaired when stimuli were presented directly to the fingers through small buzzers instead of visual stimuli on a computer monitor, the latter of which being the prevailing way of stimulus presentation in SRT tasks. As a result, implicit sequence learning cannot be fully motoric but it must also be partly stimulus-based and location-based. Witt et al. (2008) proposed that sequences are coded in *response locations* that involve the anticipation of subsequent responses at a spatial level in pursuit of a cue, that are initially effector-independent, and that may among others be coded in a spatial hand- or forearm-based frame of reference (cf. Rieger, 2004). Thus, sequence execution involves a spatial component in an egocentric frame of reference.

We continue to apply the egocentric frame of reference even after extensive practice (Witt et al., 2008). For example, De Kleine and Verwey (2009) found that the performance of the highly practiced hand is reduced when it produces the practiced sequences at a different location. Yet there is still some disagreement on which egocentric frame of reference is used for the location-specific component. Witt et al. (2008) argue that it can either be eye-, head- or torso-based, and they found that sequences were not preserved in hand space; De Kleine and Verwey (2009) pose that it is most likely stabilized to the trunk, shoulder or head; Verwey et al. (2009) however suppose that "effector-specific learning is based on the development and use of a spatial component with a hand-based reference frame" (p. 359). When Verwey and Clegg (2005) had participants learn either unimanual or bimanual sequences in an SRT task and then mirrored the sequence, they found moderate transfer from one hand to the other with unimanually learned sequences but no transfer with the bimanually learned sequences. As a result, bimanual sequences must be learned hand-independent, which would be a fundamental difference between the mental representations of one- and two-handed practice. It furthermore may involve activating another (hand-based) frame of reference to continue producing the sequence by the other hand. This, in turn, could explain why Verwey et al. (2009) found chunking to often coincide with inter-hand transitions (see their Fig. 4). They pose that sequencing either needs to be coordinated between the two hands or that a representation suitable for the fingers of each hand must be developed, by forming codings for the left and right hand separately. The latter explanation is not compatible with the coding in response locations (Witt et al., 2008; explained above), so having to coordinate sequencing between two hands seems a more likely theory, and one that could involve hand-based frames of reference interacting with one another. Do hands indeed need to coordinate sequencing together, and does this take place in a hand-based frame of reference?

This paper set out by asking why people are remarkably capable of executing bimanual skills on one location when these were learned on another. Studies by Grafton et al. (1998) and De Kleine and Verwey (2009) found that changing the position of the hand relative to the body does affect performance but that learned sequences generally transfer well to another location. The cause for this flexibility may lie in the hands coordinating the bimanual sequences by employing hand-based frames of reference (Verwey et al., 2009). If this is the case, because the frames of reference need to be readjusted in stead of the effectors, a spatial manipulation should cause both hands to perform slower over the entire sequence and at all stages of practice. This leads to the hypothesis that performance is expected to decrease equally for both hands, occurring after both little and extensive practice, and for both the effector-specific and effector-independent components.

In short, the aim of this study was to determine whether both hands perform slower after only one hand is moved. This was tested in an experiment in which participants learned two 6-digit DSP sequences. At two points in the experiment (after little and extensive practice), a spatial manipulation was introduced, in that the right forearm was moved 90° to the right. In this hand setting, the participants would repeat the same DSP sequences as in the practiced position.

Method

Participants

Twenty-four students (17 female, 7 male, *M* age = 20.96 years, *SD* = 2.01 years) from the University of Twente took part in this study in exchange for course credit. All participants were self-proclaimed right-handed. An informed consent form was signed before participation.

Apparatus

The experiment was programmed and conducted in E-Prime 2.0 on a 2.8 GHz Pentium 4 PC with 512 MB RAM running under Windows XP. Stimuli were presented on a 15” Philips 107T5 display at a refresh rate of 75 Hz, with a resolution of 640 × 480 pixels, at 16-bit color depth, and that subtended a visual angle of approximately 1°.

Directly in front of the display were placed two Trust USB keypads, embedded near each other in a black wooden mould. The keypad on the left was rotated 90° counter-clockwise, the one on the right 90° clockwise. This allowed participants to place their left hand’s little-, ring-, middle, and index fingers on the left keypad’s “/”, “8”, “5”, and “2” keys, respectively, and their right hand’s index-, middle-, ring- and little finger on right keypad’s “3”, “6”, “9”, and “*” keys, respectively. Both were connected over the same USB controller (see Appendix). The dual keypad setup was chosen so that during the practice phase the hands were placed as close together as possible, and the same input apparatuses were retained for the test phase, precluding confounding as a result of using different input devices. Because the right keypad would be fitted outside the participant’s field of view when looking ahead at the monitor during the test phases, a black letter tray occluded the participant’s sight on the keypads to preclude confounding. A chinrest was placed at 60 cm from the display to diminish any effect of the right hand being repositioned over the course of the experiment and to assure that potential head-based frames of reference did not differ across participants. The room (2.25 × 2.25 × 3.50 m) was dimly lit with fluorescent light and fitted with a webcam for monitoring purposes.

Task

Upon registering for participation, participants received the assignment to memorize two 6-digit numbers. The ability to recite the numbers from memory was a prerequisite for further participation in the experiment. One participant was rescheduled to a later time slot for not having learned the numbers. As eight fingers were used in the experiment, the digits ranged from 1 through 8, with 1 corresponding with the left little finger and 8 with the right little finger. Participants were told that only the first cue of a sequence would be presented, after which the memorized numbers served as imperatives for the subsequent keypressings desired from the participant. Cue presentation beyond the first cue was purposefully omitted in order to exclude interference from stimulus presentation remaining in the same spatial location (i.e., on the computer monitor) whilst the right hand was in a different position. High error rates in a pretest suggested that participants had great difficulty in stimulus-response (S-R) mapping when the right hand was moved to the alternate location.

For the little- (or pinky), ring-, middle-, and index finger of the left hand (“p”, “r”, “m”, and “i”, respectively) and the index-, middle-, ring-, and little finger (or pinky) of the right (“I”, “M”, “R”, and “P”, respectively), the base sequences were ipIRPm (or 4-1-5-7-8-3) and MRmprI (or 6-7-3-1-2-5). The order of the sequences was counterbalanced across participants by shifting the keypresses of each hand to the right (e.g., a keypress participant 1 executed with his left middle finger was executed with the left index finger of participant 2, the left little finger of participant 3, and the left ring finger of participant 4). Therefore, ipIRPm was counterbalanced to prMPIi, rmRIMp, and miPMRr, while MRmprI was counterbalanced to RPirmM, PIpmiR, and IMripP. Hence, the transitions between the second and third keypress and the fifth and sixth keypress are a between-hands transition. Participants were assigned over the conditions by order of participation.

Throughout all blocks, the display showed eight homogenously gray square outlines (6 × 6 mm) against a black background and with a black filling. This layout corresponds with the spatial arrangement of the assigned response keys (i.e., /, 8, 5, 2, 3, 6, 9, and *). The squares were placed adjacently in a horizontal order with 4 mm spacing or about 0.4° at 60 cm face-display distance. No additional distance was added between the fourth and fifth square, in order to prevent longer response times at between-hands intervals due to the visual structure of the stimuli. The row of squares was centered in the horizontal plane and vertically aligned at about one third from the top of the display.

The first stimulus, or key-specific cue, consisted of a square lighting up by its filling becoming bright green. Participants responded by depressing the corresponding key, after which the filling immediately returned to its neutral state with black filling. All following keypresses were to be retrieved from memory and thus were not displayed by squares lighting up (cf. De Kleine & Verwey, 2009). This series of six keypresses in a fixed order is denoted a *sequence*. Depressing a false key (i.e., failing to execute the sequence in its correct order) terminated the sequence execution and resulted in the message “Wrong key” (in Dutch) being displayed for 500 ms. After 1000 ms, a new sequence was initiated. A premature first response resulted in a message saying “Too early” (in Dutch). The next sequences started 1,000 ms after a sequence was completed or terminated. It was acceptable to release a key even after depressing the ensuing key, as key release is not being registered. Only the latency between the depression of one key and the next was registered by E-Prime, which because of the 0 ms response-cue interval are denoted the interkey intervals (IKIs).

Procedure

At the start of the experiment, an on-screen message instructed participants on which keys they were to place their fingers, and that they were to respond to each key-specific cue as rapidly and as accurately as possible by pressing the associated key. At the end of each block segment, before a pause or break, participants received an overview showing their execution and error rates for 10 s. If the error rate rose above 8%, the message “Try to respond more accurately” (in Dutch) followed the overview. This percentage was set very low in order to emphasize the importance of accuracy, as participants to the pretest made too many errors. Error rates below 3% resulted in the message “Try to respond faster” (in Dutch), in order to prevent cautious and therefore slow keypressing that would not reflect the participant’s true sequence production skill. The experimenter helped the participant attain a position that would remain comfortable even when the right forearm was turned 90° outward.

The experiment consisted of nine blocks that participants performed in a single session. The experiment commenced with a single practice block (Block 1), in which both keypads were placed in front of the participant. Each practice block in this experiment was composed of an 80-trial sub block, a 20-s break to relax one’s muscles, and another 80-trial sub block. At the end of each block, a message informed the participant the block had finished and instructed to wait for the experimenter. The time in between finishing a block and starting the next block averaged 4 min. If necessary, the experimenter would encourage the participant to improve sequence execution by responding faster or more accurate. Following all breaks, there was a 1,000 ms interval between the squares being redrawn and the onset of the first key-specific cue.

Block 2 was the first test block. By then, all participants had learned to translate the 6-digit code into motor actions. Test blocks were composed of two 40-trial sub blocks separated by a break that the experimenter terminated manually. The sub blocks differed in the position of the right keypad, which was either in front of the participant as with the practice blocks or placed in a mould 90° to the right (relative to the shoulder). Sub blocks were counterbalanced between participants and conditions, meaning that half of the participants started with the right keypad to the right and finished the test block with the right keypad in front of them and the other half of the participants vice versa. Participants then executed six consecutive practice blocks (Blocks 3 through 8). Together with the first practice block, the practice phase amounted to 1120 trials, or 560 trials per sequence. It is generally agreed upon that effector specificity has developed after a sequence was practiced at least 500 times (Rhodes et al., 2004).

At the end of the experiment was the second test block (Block 9), which was identical to the test block early in the experiment. Participants who started Block 2 with the right keypad placed 90° to the right, now also started in this condition. After finishing the ninth block, participants filled out a paper questionnaire, that started out by asking whether participants could reproduce in writing the two sequences they had been trained with (‘free recall’), then required them to select these sequences out of a set of 12 alternatives (‘forced choice’), and finally, to indicate what strategy they used to reproduce the sequences for the questionnaire: (a) by remembering the order of the letters on the keys, (b) by remembering the order of the stimuli on the screen, (c) by ticking the sequence with their fingers on the table or in memory, or (d) in another way. In order to measure actual sequence knowledge, the ‘free recall’ measure forced participants to translate the sequences into keypresses rather than recalling the 6-digit numbers they had memorized prior to the experiment. Participants were finally debriefed by an explanation that nothing other than performance was measured during this experiment.

Data analysis

Excluded from RT analysis were the first two trials of each sub block, sequences in which an erroneous key was depressed, and outliers. Outliers were considered those sequences that differed 3 *SD* from the mean. This excluded 1.8% of the sequences. For error analysis, all erroneous keypresses except the first two trials of each sub block were counted and divided by the total number of trials in each block, to obtain error rates per keypress (R1 through R6) per block. For statistical analysis, error rates were arcsine transformed using the formula $X'_{ijk} = 2\sin^{-1}[(X_{ijk} +$

$1/(2n)]^{½}$ (Winer, Brown, & Michels, 1991, p. 356), where n is the number of times a keypress within a sequence was executed per block (i.e., 80 for practice blocks, 40 for test blocks).

The primary performance measure of interest with DSP sequences is the time (in milliseconds) between each keying response. These are denoted the initiation interval (T1) for the response to the first cue and interkey intervals (IKIs; T2 through T6) for the five consecutive responses. The interval numbering (i.e., T1 through T6) thus provides an index of their serial position within the sequence. Interkey intervals were further subdivided into (within-hand or effector-specific) execution intervals (i.e., T2, T4 and T5) and (between-hands or effector-independent) transition intervals (i.e., T3 and T6). Both sequences had the same structure, though one started with the left hand and the other with the right. For the instances in which the sphericity assumption of the F-test was violated, the Greenhouse-Geisser ε was used to correct the values of the degrees of freedom.

Results

Explicit sequence learning

Directly following the experiment, 22 participants were able to correctly recall all six elements of both practiced sequences in free recall. This means there was a high degree of explicit sequence knowledge, which was facilitated by the (explicitly) prelearned sequences.

Practice phase

Insert Figure 1 about here.

Although the two learned sequences were different in which hand executed a particular keypress, a 7 (Block: 1, 3 – 8) × 2 (Sequence: 1 & 2) × 6 (Key: T1 – T6) repeated measures ANOVA showed that there was no main effect of Sequence, $F(1, 23) = 2.16, p = .16$. So sequences could be considered similar for further analysis. Analysis on the practice blocks was now conducted using a 7 (Block: 1, 3 – 8) × 6 (Key: T1 – T6) repeated measures ANOVA. Results showed participants became faster through practice, yielding a significant main effect on Block, $F(6, 18) = 60.67$, $p < .001$. Figure 1 shows how the sequence representation was separated in two distinguishable segments, or motor chunks. This was also supported by a significant Block*Key interaction, $F(2.65, 60.99) = 8.40$, $p < .001$. A planned contrast investigating whether T3 deviated from T2 – T6 confirmed that T3 was indeed slower over all practice blocks, $F(1, 23) = 23.52$, $p < .001$. In both sequences, T3 and T6 were between-hands transition intervals, locations where chunking often coincides with (Verwey et al., 2009). This is why T6 was contrasted with T2,4,5,6 over all practice blocks, which indicated that T6 was not slower than the within-hand execution intervals but faster instead, $F(1, 23) = 26.57$, $p < .001$. So there were no indications that a chunk has been formed at this transition interval at any point in the experiment.

Test phase

Insert Figure 2 about here.

Performance in the test blocks were analyzed using a 2 (Block: 2, 9) × 2 (Position: familiar vs. new) × 6 (Key: T1 – T6) repeated measures ANOVA. A significant main effect on Block confirms that practice led to faster sequence execution, $F(1, 23) = 155.66$, $p < .001$. The Block*Position interaction was not significant, $F(1, 23) < 1$, which suggests that with both little and extensive practice, sequence execution of both hands was similar when the right hand was moved to the new position. The main effect of Position was significant, $F(1, 23) = 9.24$, $p < .01$, which showed that both sequences were executed slower after the right forearm was moved outward (Fig. 2). But does this performance decrease pertain to only the moved hand or are both hands affected? This was assessed using two 2 (Position: familiar vs. new) × 2 (Hand: right vs. left) × 6 (Key: Seq1 T1,2,6 + Seq2 T3,4,5 for the right hand; Seq2 T1,2,6 + Seq1 T3,4,5 for the left hand) repeated measures ANOVAs separately for Block 2 and 9. The main effect of Hand was not significant in either Block 2, $F(1, 23) = 1.23$, $p = .28$ or Block 9, $F(1, 23) < 1$. Thus, following a spatial manipulation where one hand was moved, both hands are slowed equally great regardless of the amount of practice (Fig. 3).

Insert Figure 3 about here.

Did the effector-specific execution intervals (T2, T4 and T5) become slower with a change in hand position but not the initiation interval (T1) or the effector-independent transition intervals (T3 and T6)? This was investigated using paired-samples *t*-tests for both sequences independently in blocks 2 and 9, comparing the individual keypresses on the familiar and new position, resulting in a Bonferroni corrected critical *p*-value of .008. No keypress reached significance. So the data do not suggest a difference between performance on initiation, execution and transition intervals.

Errors

Mean error rates per keypress amounted to 10.6% in the first block where participants translated the numbers they learned into motor actions. In the other practice blocks (3 through 8), on average 5.6% of the keypresses were erroneous. In the first test block, after little practice, mean error rates were 1.9% in the familiar hand position and 2.2% in the new hand position. With extensive practice, error rates in the second test block averaged 2.8% in the familiar hand position and 3.2% in the new hand position.

Errors were analyzed using a 9 (Block: 1 – 9) × 6 (Key: T1 – T6) repeated measures ANOVA. Error rates increased per keypress, from 1.1% at R1, to 1.7%, 3.1%, 4.5%, 5.8%, and 6.5% for R2 through R6, respectively, yielding a highly significant main effect of Key, $F(1.93, 44.37) = 195.89$, $p < .001$. A significant main effect on Block indicates a higher than average error rate on Block 1 and fewer errors in the test blocks, $F(3.58, 82.22) = 21.42$, $p < .001$. The Block*Key interaction was also significant, $F(9.05, 208.03) = 11.53$, $p < .001$, which shows that the error rates per key were very different across blocks. These results suggest that errors in sequence execution are associated with the serial position of a response within a sequence.

Error rates in the test blocks were analyzed using a 2 (Block: 2, 9) × 2 (Position: familiar vs. new) × 6 (Key: T1 – T6) repeated measures ANOVA. A significant main effect of Block is indicative of an increase in errors after extensive practice, $F(1, 23) = 8.14$, $p < .01$. Error rates did not differ between the new and familiar hand position, $F(1, 23) < 1$.

Discussion

This experiment set out to investigate whether both hands suffer equally in terms of RT from moving only one hand. Previous studies have found unimanual sequences to transfer well to other spatial settings, albeit with a decrease in execution speed (Grafton et al., 1998; De Kleine & Verwey, 2009). Besides confirming that these findings do also extend to bimanual sequence learning, the data from this study show that the performance decrease in bimanual sequences following a spatial manipulation is equal for both hands, while only one hand was moved. Execution of the entire sequence was slowed and this effect already occurred after little practice. Neither was there a change in error pattern. These results show that a spatial manipulation must affect a component that is already present early in sequence learning, which precludes the possibility that it is related to the development of effector-specificity. Instead, a spatial manipulation appears to affect the frame in which the effectors are grouped; i.e. the hand-based frame of reference. The new setting thus requires the frames of reference of both hands to adjust to one another, both with equally much effort. Just as the hand-based frames of reference have previously been associated with transfer of sequence knowledge to other effectors (Witt et al., 2008), this could be another strategy to quickly adapt to a change in context. The hands would still collaborate in relatively the same way, though at a lower pace. In other words, when adapting to a change in context, continuity is retained while efficiency is slightly impaired.

Did the hand-based frames of reference also overlap, in that they shared their frames of reference? Slowing for both hands was equally great for both hands after sequences practiced with both hands placed adjacently were executed with both hands placed apart, even though only one of the hands was moved, only the right hand was dominant and each hand initiated a different sequence. None of these differences appear to have affected performance. So the cause of slowing either must lie in (a) the position of one hand-based frame of reference relative to the other, or (b) the shared hand-based frame of reference getting separated. The between-hands transition intervals were not impaired more greatly following the spatial manipulation and T6 was consistently performed quickly throughout the experiment (discussed below). These findings show that the slowing was not associated with the activation of another hand-based frame of reference either, so the data from this experiment indeed suggest a shared hand-based frame of reference.

Earlier research by Verwey et al. (2009) found that chunking predominantly, but not always, coincides with inter-hand transitions. Exceptions were only present in sequences that had at least one other transition interval where chunking occurred. This experiment found similar results. There were two transition intervals, T3 and T6. Chunking had quickly developed at T3 but execution at T6 was even faster than at any other point within the T3 – T6 chunk. Hands appear quite capable of coordinate sequencing between one another, even without practice. The transition interval T3 imposed the start of a new chunk, and it subsequently was perhaps more cost-efficient to chunk the sequences as 2-4 rather than 2-3-1, meaning that T6 is added to the T3 – T5 chunk to form a 4-key chunk. Execution of three keypresses by one hand was supplemented with a keypress by the other hand without a problem, probably by the concatenating processor. This does give rise to the question whether chunk length is governed by the need to fine-tune sequence production to the biomechanical properties of a hand (cf. Berner & Hoffmann, 2009b). Future research using bimanual sequences with only a transition interval at T3 could determine whether participants would execute T3 through T6 as a 4-key chunk with a single hand. It may well be that chunking will then take on a 2-2-2 pattern, because a 4-key within-hand chunk has a detrimental effect on efficiency because the effectors all tap into parts of the same biomechanical system, whereas effectors of the other hand do not.

In this study, right-handed participants moved their right (i.e., dominant) hand, because it was expected to adapt more easily to other hand settings. Therefore, if an effect were found in this setting, it would be likely that it also applies to the event that the nondominant hand is moved. Further research should look into whether these same effects can be replicated, although it may yield different results, as the dominant hemisphere may have affected the way participants could adapt to a different spatial setting, because it has a significant role in controlling the nondominant arm but not vice versa (Haaland & Harrington, 1996), and sequence knowledge from the dominant hand can generalize to the nondominant hand but not vice versa (Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003). Generalization can thus only occur from the dominant to the nondominant arm, as cells in the non-dominant hemisphere that participate in sequence learning are not tuned to movements with the ipsilateral arm (Criscimagna-Hemminger et al., 2003).

This research investigated the way the brain develops bimanual skills that adapt fairly well to changes in the spatial context, such as playing music on multiple keyboards or controlling very diverse aspects in a virtual game environment. Both hands were found to be equally impaired over the entire sequence following a spatial manipulation, which provides evidence that for bimanual sequence execution, hand-based frames of reference are employed. The pattern of slowing indicates that the hand-based frames of reference may even overlap. In line with previous research, it was found that the brain prefers to chunk at between-hands transition intervals but that it is also highly capable of letting a chunk consist of keypresses by both hands, provided a sequence already involved one other transition interval. In conclusion, this research found evidence for the use of hand-based reference frames in bimanual sequence execution that may also overlap. This strategy allows us to transfer our learned movements to other settings, just as keyboardists and gamers do.

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Appendix

Variance of USB input devices in RT testing

Sequence learning experiments have long been using PS/2 keyboard connectors, which added approximately 19 ms to the error variance.[1] This experiment required the use of two separate smaller keyboards, or keypads, that are now more commonly available with Universal Serial Bus (USB) connectors. Connecting several input devices via USB is feasible, because most modern PCs include several USB ports. USB and Firewire hardware communicate with software through a *host controller interface* (HCI), which is controlled through a *host controller driver* (HCD) on the software side.[2] Various HCIs for USB currently exist, which can all coexist on a single PC:

1. *Universal HCI* (UHCI) is Intel's proprietary interface for USB 1.x, used commonly on Intel, VIA and OPTi chipsets. Intel also created a wireless interface (WHCI).
2. *Open HCI* (OHCI) is the open standard interface for USB 1.x, used in add-in cards and chipsets not based on Intel, VIA or OPTi.
3. *Enhanced HCI* (EHCI) handles only the high-speed controlling of USB 2.0 and 3.0. It relies on UHCI or OHCI for the low- and full-speed USB 1.x handling.

There is relatively much happening that can introduce latencies.[3] Keyboards and keypads are low-speed devices and always connect over USB 1.x, which means their input is processed

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[1] Segalowitz, S. J., & Graves, R. E. (1990). Suitability of the IBM XT, AT, and PS/2 keyboard, mouse, and game port as response devices in reaction time paradigms. *Behavior, Research Methods, Instruments, and Computers, 22*, 283-289.

[2] Wikipedia (2010). *Host controller interface*. Retrieved June 11, 2010, from http://en.wikipedia.org/wiki/Host_controller_interface

[3] M. Lotz, personal communication, September 26, 2009.

through either UHCI or OHCI. It is possible to force the use of EHCI by using a USB 2.0 hub but this introduces more intermittent physical components and protocols, thereby causing additional (unwanted) latencies. As low-speed devices, their poll rates are comparatively low, usually reporting input about once every 8 ms. The UHCI and OHCI protocols do also process data differently; UHCI does less on the hardware side and requires more CPU processing, whereas OHCI feeds more intelligence into the interface.[4] There are also marked differences between USB keyboards. When testing device latency in ms of various input devices on several system settings, Psychology Software Tools found a Dell USB keyboard to have very little latency (averaged $M = 16.94$, $SD = 4.77$), whereas the latency of a Belkin USB keyboard was much greater (averaged $M = 43.02$, $SD = 3.67$).[5] Furthermore do the upper layers of the operating system introduce quite a bit of possible latency, although since the different threads will be woken up by the notifications, they should run through pretty directly. So possible causes of latencies in RT measurement per device are a device's properties, the HCI protocol used, and upper layers in the operating system.

With the use of multiple keyboards, serial processing may introduce additional latencies. If two devices provide input simultaneously over the same USB connector, the device that is scheduled for transfer earlier is handled first. Pending transfers over one connector are thus processed in a serial list but the other device's input is retrieved only a few milliseconds later. Input from separate controllers is handled in parallel but if they are connected differently to the motherboard (e.g., onboard, pins, PCI), the physical differences may also introduce latencies. The

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[4] Wikipedia (2010). *Host controller interface*. Retrieved June 11, 2010, from http://en.wikipedia.org/wiki/Host_controller_interface

[5] Psychology Software Tools. (2006). Response device tests: E-Prime 1.2 stimulus device response timing values. Retrieved August 20, 2009, from http://www.pstnet.com/eprimedevice.cfm

use of different devices, connecting them via the same USB connector or via physically different USB connectors, or letting the devices be processed by different HCI protocols may all introduce latencies with the use of two or more USB input devices.

In conclusion, to ensure the best results with a minimum of latency per device and a minimum of difference in latency between devices, use the exact same type of USB device and preferably connect these to separate HCI controllers with fully identical physical properties (thus also using the same interface). Alternatively, the same controller may be used as the serial processing of the input adds only a few milliseconds to the error variance. The experiment reported here used a single OHCI controller due to regulatory and technical limitations.

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Correspondence concerning this article may be addressed to Eddy C. Groen, University of Twente, Faculty of Behavioral Sciences, c/o Jeanine Lodeweges-De Vries, Cubicus C337, PO Box 217, 7500 AE Enschede, The Netherlands.

Figure Captions

Figure 1. Mean response time per keypress across the two practiced sequences for the practice blocks (solid lines) and the familiar hand position of the test blocks (dotted lines) as a function of serial position, showing a similar execution pattern across all blocks.

Figure 2. Mean response time per keypress across the two practiced sequences in the test blocks 2 (little practice) and 9 (extensive practice) for the familiar and new hand positions. Sequence execution was slower after a spatial manipulation.

Figure 3. Mean response time across the two practiced sequences in the test blocks 2 (little practice) and 9 (extensive practice) as a function of hand configuration and performance of the individual hands. Both hands were slowed following a spatial manipulation.

Figure 1

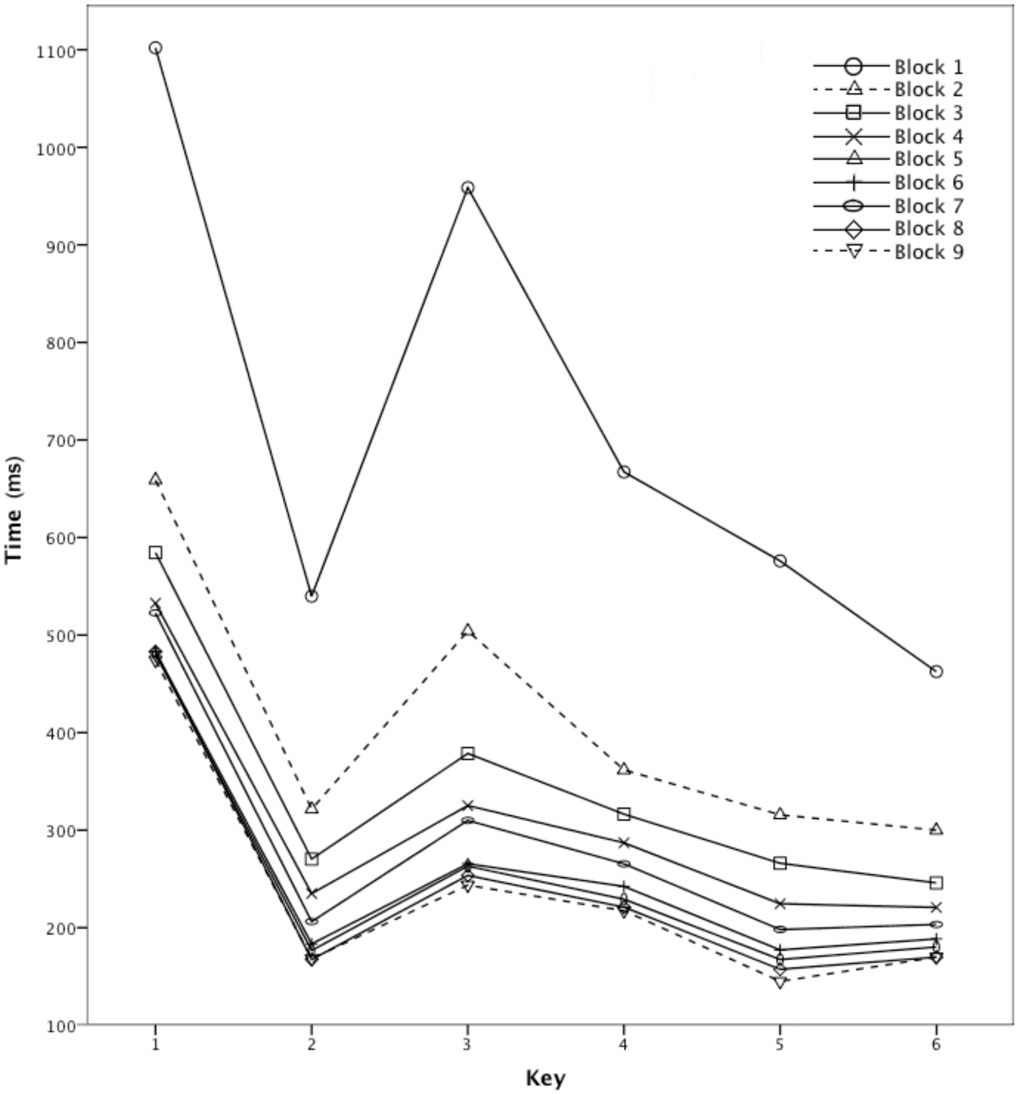

Block 1
Block 2
Block 3
Block 4
Block 5
Block 6
Block 7
Block 8
Block 9
Time (ms)
1100
1000
900
800
700
600
500
400
300
200
100
Key
1
2
3
4
5
6

Figure 2

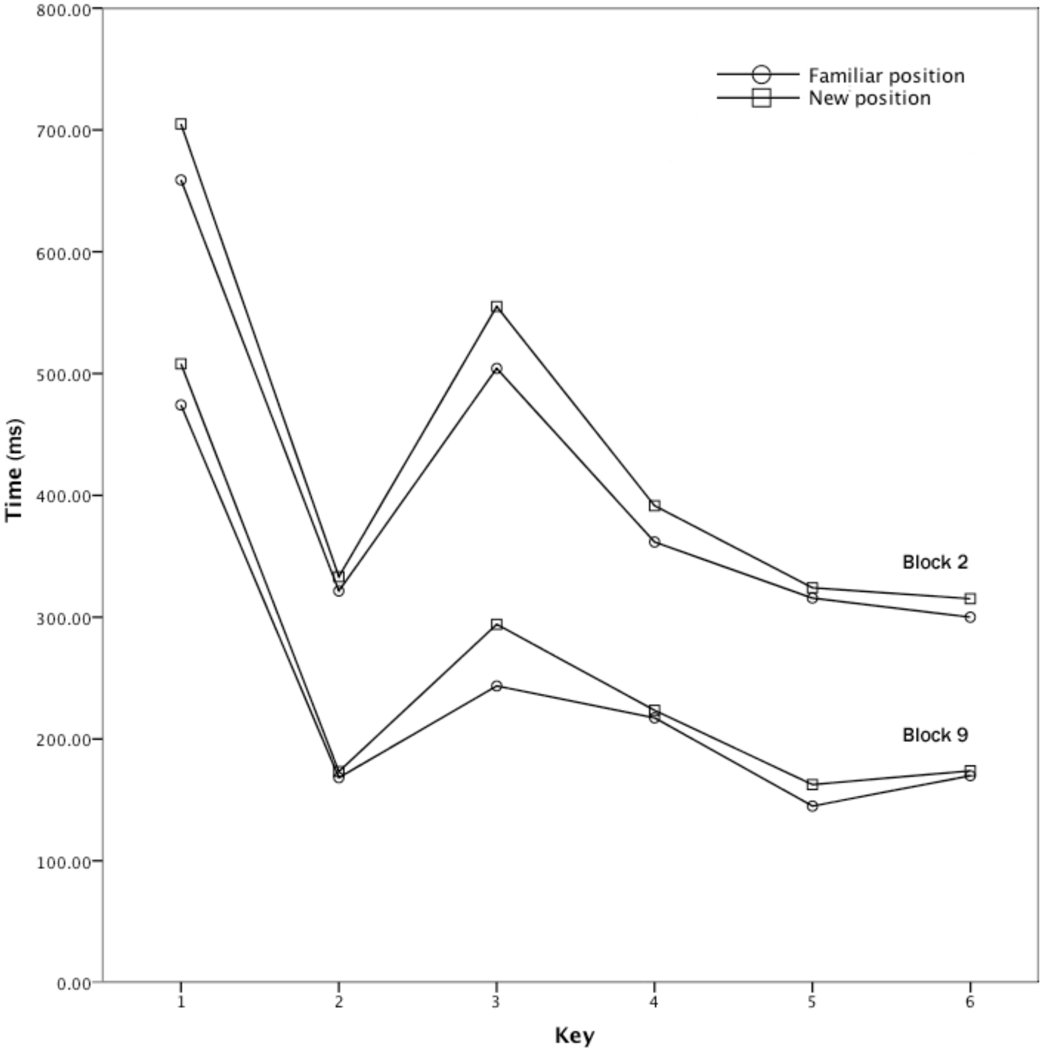
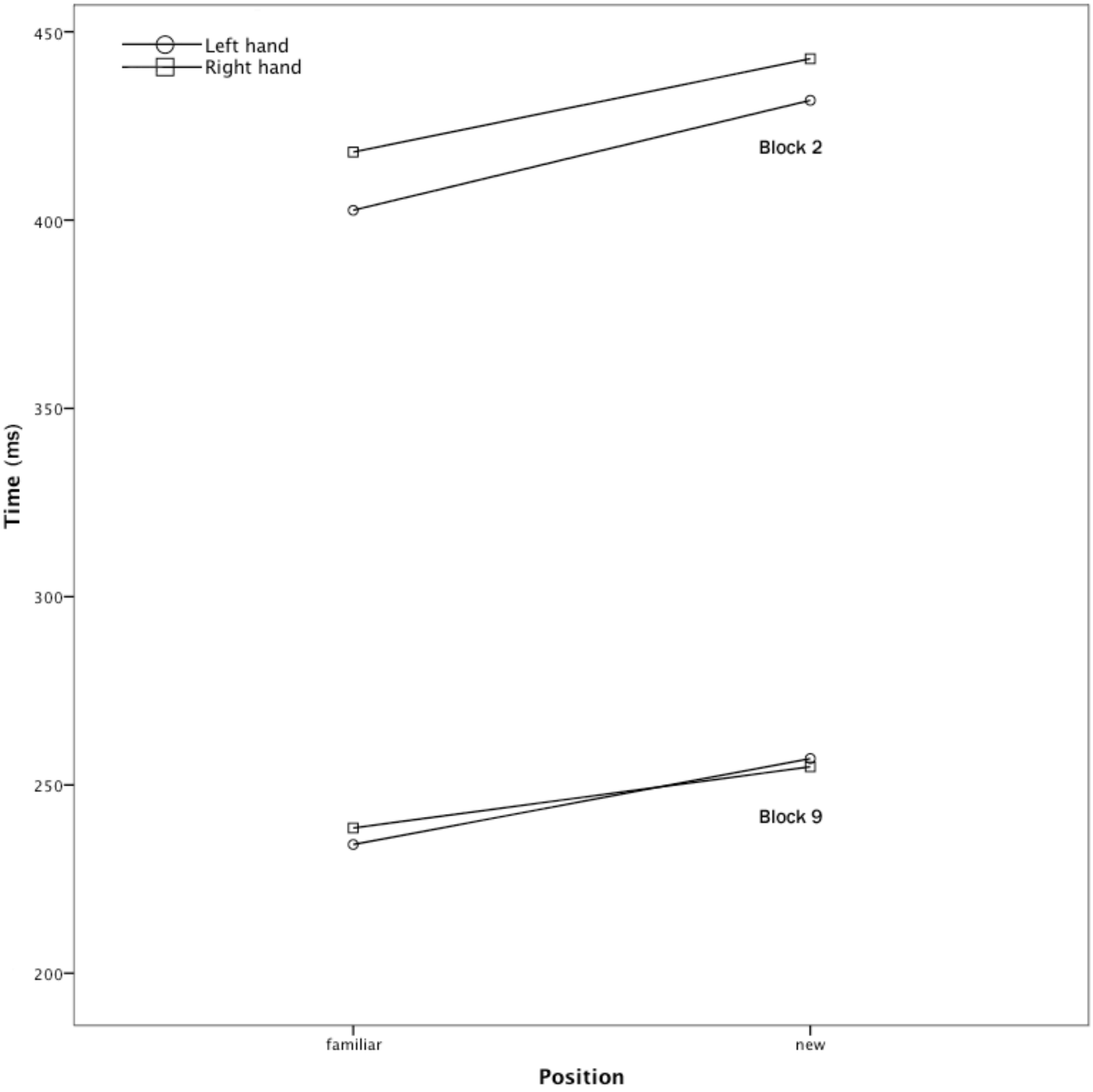

800.00
700.00
600.00
500.00
400.00
300.00
200.00
100.00
0.00
Time (ms)
1
2
3
4
5
6
Key
Familiar position
New position
Block 2
Block 9

Figure 3


Left hand
Right hand
Block 2
Block 9
Time (ms)
450
400
350
300
250
200
familiar
new
Position