Sensory and motor components of highly skilled action sequences

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Note

Experiments 1 and 2 of this thesis will be published in *Psychological Research* in an article entitled "Effector-related sequence learning in a bimanual-bisequential serial reation time task".

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1 Abstract

A series of experiments was conducted in order to investigate motor contributions to learning highly skilled action sequences in contrast to sensory contributions. Experiments 1–4 made use of a bimanual-bisequential variant of the serial reaction time task: Presentation of imperative stimuli was arranged such that participants' left-hand and right-hand responses followed different sequences independently of one another, thus establishing a compound sequence spanning both hands. At least partly independent learning of the two concurrently implemented hand-related sequences was demonstrated after extensive practice under conditions of both simultaneous (Experiments 1 & 2) and alternating (Experiments 3 & 4) stimulus presentation and responding. It persisted when there was only one imperative stimulus for presenting both hand-related sequences (Experiments 2–4) instead of two separate imperative stimuli (Experiments 1 & 2), one for each sequence, even when the hand-related sequences were correlated and massive integrated learning of the compound sequence occurred (Experiment 4). As for the nature of the independently acquired sequence representations, transferable sequence knowledge was acquired only when there was a separate imperative stimulus for each sequence (Experiments 1 & 2) but not otherwise (Experiments 2–4). The most likely stimulus-based representations which allow for intermanual transfer can be regarded as sensory components of highly skilled action sequences, whereas motor components can be considered as being reflected in effector-specific, non-transferable sequence knowledge. The same decomposition logic applies to transferable and non-transferable sequence knowledge observed under conditions of unimanual practice of a single sequence (Experiments 6 & 7). The advantage of practicing a key press sequence with fingers of one hand as opposed to practicing it with fingers of both hands (Experiment 5) also implicates a motor component as the two assignments were equivalent in all other respects. Moreover, Experiments 6 and 7 showed that hand-specific sequence knowledge can develop after relatively little practice (as little as approximately 120 sequence repetitions). Presumably, this occurs especially in tasks with particularly pronounced requirements for coarticulation between consecutive finger movements. In sum, the present series of experiments provides compelling evidence for an effector-specific component of sequence learning. Albeit relatively small in size, it emerged consistently under various conditions. By contributing to the refinement of sequential action execution it can play a role in attaining high levels of performance.

2 Introduction

All behavior is sequential, that is, it consists of ordered sequences of actions. This is true for mundane tasks like brewing coffee as well as for highly complex ones like speaking. Repeatedly executing a sequence of actions typically refines and improves performance, indicating the development of sequencing skill. The capacity for sequence learning is highly adaptive and one of the characteristic features of human cognition (e.g., Lashley, 1951).

Oftentimes, behavior involves multiple effectors used in concert to respond concurrently to different aspects of the environment or to produce a desired effect. For example, fingers of the left and the right hand are usually involved in playing a song on the piano. Likewise, dancing while singing requires the execution of leg and arm movements concurrently with movements of the vocal tract. When considering such multi-effector sequential actions, the question arises whether knowledge about its effector-related components (e.g., the sequence of left-hand movements and the sequence of right-hand movements) might be acquired and represented at least partly independently of each other or whether the compound sequence spanning all involved effectors is stored in memory in an entirely integrated fashion.

More specifically, the hypothesis that sequence learning might depend to some extent upon the effectors used can be broken down into two related aspects: As just stated, (1) effector-related sequences might be acquired at least partly independently of one another as a consequence of their being executed with different effectors. Obviously, this entails the possibility that (2) independent knowledge about effector-related sequences might be stored in an effector-specific manner so that it is not transferable from the effector used during training to another effector. However, independent learning of effector-related sequences sequence does not necessitate that acquired sequence knowledge is effector-specific. The issue of effector specificity of sequence knowledge also applies to sequential actions involving only a single effector, and it has already been the subject matter of numerous studies (e.g., Deroost, Zeeuws, & Soetens, 2006; Jordan, 1995; Keele, Jennings, Jones, Caulton, & Cohen, 1995; Park & Shea, 2005; Verwey & Clegg, 2005). In contrast, independent learning of effector-related sequences has not yet been investigated systematically.

Research and theorizing relevant to (a) independent learning of concurrent sequences and to (b) effector-specific sequence knowledge will be reviewed in turn. I will begin, however, by briefly introducing the most prominent model task for investigating sequence learning in the laboratory, the serial reaction time task.

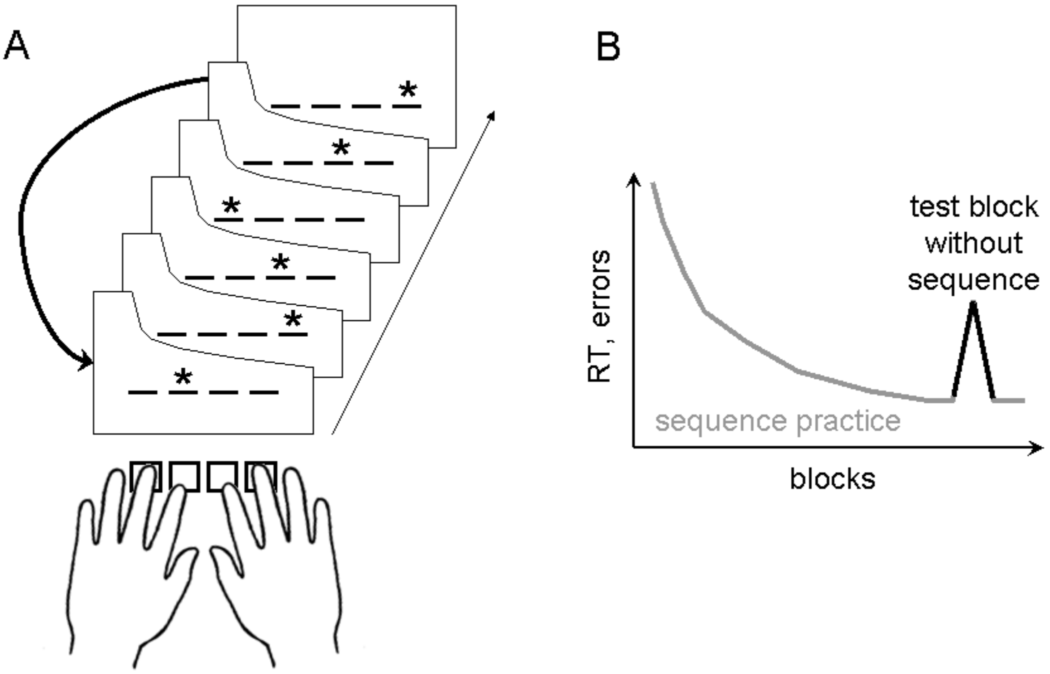

Figure 1. Illustration of the typical setup in an SRT experiment. Participants respond to spatial imperative stimuli by pressing compatibly assigned keys; the stimuli appear in a cyclically repeating sequence as indicated by the arrow on the left-hand side (A). Learning of the sequence is assessed after a period of practice by replacing the practiced sequence with an unpracticed or a random sequence; a decrement in performance in this test block relative to adjacent sequence blocks indicates sequence learning (B).

2.1 Investigating Sequence Learning with the Serial Reaction Time (SRT) Task

Since its introduction by Nissen and Bullemer (1987) the serial reaction time (SRT) task has become the dominant tool for researchers aiming to further understand the mechanisms underlying sequence learning. On each trial in a typical SRT experiment (see Figure 1A), a stimulus appears in one of several locations, and participants are instructed to press the key assigned to that location as soon as possible. The key press terminates the current trial, and the next trial is initiated (i.e., the next imperative stimulus appears). The critical manipulation entails the implementation of structural redundancies, for example, the presentation of the stimuli in a fixed repeating sequence. Although participants are not informed about the presence of regularities in the task, speed and accuracy of their responses typically improve over the course of many sequence repetitions (e.g., Nissen & Bullemer, 1987). However, these benefits associated with practice might not only reflect sequence learning but also improvements in the ability to deal with general aspects of task performance unrelated to the presence of a sequence. In order to obtain a maximally pure measure of knowledge acquired specifically about the sequence, learning of the sequence is tested by presenting a random or an unpracticed sequence instead of the practiced sequence. A decrement in performance in such a test block compared to preceding or following regular blocks is used as a measure of sequence learning (see Figure 1B).

Sequence learning as indicated by performance decrements upon abolishment of the sequence has also been observed for participants who in a post-experimental interview or task failed to recall or even recognize the sequence present during the experiment or substantial parts of it (e.g., Curran & Keele, 1993; Willingham, Nissen, & Bullemer, 1989). Indeed, the SRT task has been used frequently to investigate implicit learning (e.g., Jiménez, Vaquero, & Lupiánez, 2006; Perruchet & Amorim, 1992).

2.1.1 *Characterization and Types of Sequence Structures*

Traditionally, demonstrations of sequence learning in SRT experiments have used fixed repeating sequences (e.g., Nissen & Bullemer, 1987; Reed & Johnson, 1994). Obviously, the rate of learning will depend on the complexity of the sequence. The regularity inherent in sequences can be characterized by the probability of transitions between events. An n^{th}-order transition probability $P(E|A_n, \dots A_2, A_1)$ is defined as the relative frequency of the occurrence of event E on trial t following the sequence of events $A_n, \dots A_2, A_1$ on trials $t–n, \dots t–2, t–1$ among all occasions on which that particular sequence of events occurs (see Remillard, 2003; footnote 1, p. 581).[1] For example, in the sequence JMKJLKML the 1st-order transition probability for "K after M" is 50% because K follows event M on one occasion, but event M is also followed by event L on another occasion, so that $P(K|M) = ½$. This means that the sequence is not completely predictable at the level of 1st-order transitions. However, the example sequence is completely predictable at the level of 2nd-order transitions because for each pair (2-tuple) of successive events there is only one successor event, so that $P(K|JM) = 1$, $P(J|MK) = 1$, $P(L|KJ) = 1$, etc. Such sequences are called second-order conditional sequences. It is impossible to learn second-order conditional sequences based only on direct pairwise associations. As another example, consider the sequence WXZYXYZ, which has one unique 1st-order transition ("X after W"), whereas the remaining transitions are 2nd-order transitions ("Z after WX", "Y after XZ", etc.). A sequence such as this, including both unique 1st-order and higher-order transitions, is called a hybrid sequence (Cohen, Ivry, & Keele, 1990). An-

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[1] The structure inherent in a sequence of events can also be captured concisely in terms of redundancy as defined in information theory (Shannon & Weaver, 1949). The redundancy metric provides a global measure of the amount of regularity or certainty inherent in a given situation. For a brief exposition of the application of information theoretical concepts in the domain of sequence learning see Hoffman and Koch (1998; pp. 164–168). In contrast to the redundancy metric, separately considering transition probabilities for each event provides detailed information about which parts of a sequence possess particularly high or low levels of uncertainty.

other notable aspect of the sequence is that event W occurs only once, whereas the events X, Y, and Z occur twice. Consistent with the terminology used for higher-order transitions, such basic frequencies of occurrence of single events can be referred to as 0^{th}-order probabilities.

Sequence learning has also been shown for probabilistic sequences (e.g., Cleeremans & McClelland, 1991; Remillard & Clark, 2001; Schvaneveldt & Gomez, 1998), for which transition probabilities reach a maximum at a certain order level, but never reach 1 (some transitions might never occur). For example, the 2-tuple of events KL might be followed by event M in 80% of occasions and by event K in the remaining 20% of occasions but never by event J. Sequence learning under such conditions is indicated by shorter reaction times (RTs) for the more probable succeeding events than for the less probable succeeding events. For probabilistic sequences for which all legal transition probabilities reach a maximum of 50% at a certain order-level, sequence learning is demonstrated if randomly inserted events which violate the constraints imposed by the probabilistic rule elicit longer RTs than legal transitions (e.g., Deroost et al., 2006).

It has also been demonstrated that, beyond these statistical properties, relational and temporal structure in sequences – for example, reversals (MLKKLM) or repetitions (JKLJKL) or pauses between sequence elements (JKL–JKL vs. JK–LJ–KL) – can profoundly influence sequence learning by way of facilitating chunking of sequences into subsequences (e.g., Hoffmann & Sebald, 1996; Koch & Hoffmann, 2000a; 2000b; Stadler, 1992; see also Hoffmann & Koch, 1998).

2.1.2 The Contents of Mental Sequence Representations

Because of the nature of a typical SRT task, a sequence of stimuli (S_1-S_2-S_3 ...) is confounded with a sequence of responses (R_1-R_2-R_3 ...) as well as with regularities between responses and subsequent stimuli (R_i-S_{i+1}). Therefore, performance benefits for structured sequences can result because participants learn to anticipate forthcoming stimuli on the basis of previous stimuli (S-S learning) or on the basis of previous responses (R-S learning) as well as because they learn to prepare forthcoming responses in advance (R-R learning). Indeed, there is evidence that each of these regularities contributes to sequence learning.

Some experiments have shown learning of stimulus sequences (S-S, e.g., Clegg, 2005; Frensch & Miner, 1995; Koch & Hoffmann, 2000a, 2000b; Remillard, 2003). For example, Frensch and Miner (1995) demonstrated learning of a sequence of letters and graphic symbols although the sequence of keystrokes executed by participants in response to the stimuli was random. The sequence of responses was random because the stimulus-response assignment shown at the bottom of the computer screen was changed on a trial-by-trial basis. As a consequence, sequence learning based on R-R or R-S learning can be ruled out (see also Goschke, 1998). Learning of stimulus sequences resulting solely from observation has been reported (J. H. Howard, Mutter, & Howard, 1992) but is not undisputed (e.g., Kelly & Burton, 2001; Kelly, Burton, Riedel, & Lynch, 2003).

Other experiments have shown learning of response sequences (R-R, e.g., Deroost & Soetens, 2006a; Hoffmann & Koch, 1997; Hoffmann, Martin, & Schilling, 2003; Hoffmann & Sebald, 1996; Nattkemper & Prinz, 1997; Rüsseler, Hennighausen, & Rösler, 2001; Rüsseler & Rösler, 2000). For example, Rüsseler et al. (2001) implemented a sequence of stimuli in a matrix of 2 rows and 4 columns with both cells in each column assigned to the same response. This setup made it possible to introduce two kinds of deviant stimuli into the sequence: Those that violated the sequence of stimuli but preserved the sequence of responses (perceptual deviants; stimuli appearing in the regular column, but in the irregular cell), and those that violated the stimulus sequence as well as the response sequence (motor deviants; stimuli appearing in an irregular column). Only the latter, but not the former disrupted performance. However, the finding that transitions between responses are learned does not imply that sequence knowledge is represented in a format that is specific to one set of muscles. The issue of effector specificity of sequence knowledge will be discussed in detail below.

Still other experiments revealed the impact of response-effect regularities on sequence learning (R-S, e.g., Hazeltine, 2002; Hoffmann, Sebald, & Stöcker, 2001; Stöcker & Hoffmann, 2004; Stöcker, Sebald, & Hoffmann, 2003; Ziessler, 1998; Ziessler & Nattkemper, 2001). For example, Stöcker et al. (2003) found that tone effects, appearing upon a key press and terminating prior to the presentation of the next imperative stimulus, improved sequence learning when they were mapped to response keys contingently and compatibly, relative to conditions with non-contingent, with incompatible, or without tone effects. These findings highlight the importance of anticipated action-effects or intended goals of actions as critical representations on which sequence learning can operate. An impact of action-effect relationships on sequence learning need not be restricted to experimental situations such as the one described, in which distinct tone effects were purposely added, but can be thought of as being pervasive. For example, the appearance of the next stimulus in the sequence can also be thought of as the effect produced by the previous response (cf. Ziessler, 1998; Ziessler & Nattkemper, 2001).

Going beyond the view of a strictly stimuli- and response-based representational nature of sequence learning, Willingham and colleagues have argued that learning of a sequence of response locations plays a role in sequence learning in SRT task experiments (Willingham, Wells, Farrell, & Stemwedel, 2000; see also Willingham, 1999; Witt & Willingham, 2006): Willingham et al. (2000) had participants respond with the index finger of their dominant hand on a keyboard with 4 keys. Those participants that were subsequently switched to a keyboard with 4 keys in a different layout showed no more sequence knowledge than control participants who had never seen a sequence in the course of the experiment, whereas sequence learning was evident in participants who continued using the same keyboard. Recently, Deroost and Soetens (2006b) showed that a sequence of response selections can also contribute to overall sequence learning.

In sum, it appears that representations of sequence knowledge encompass multiple layers of information, including goals, stimulus features, as well as properties of or associated with responses such as response location to name but a few (cf. Clegg, DiGirolamo, & Keele, 1998). The notion that regularities at different levels contribute to sequence learning evokes the issue of the degree to which these regularities are learned independently of one another or in an integrated fashion.

2.2 Independent Learning of Sequences

Operationally defined, learning a sequence (A) independently of another concurrently encountered sequence (B) entails that participants can benefit from the presence of that sequence (A) irrespective of whether the other sequence (B) is present in its original form, has changed, or is otherwise no longer available. Theoretically, this implicates that separate representations of the two sequences have been acquired. In contrast, integrated learning entails that aspects of both sequences are incorporated into a single unified representation so that, operationally, changes in one of the two sequences affect performance negatively even if the other sequence is in fact maintained.

The interplay between independent and integrated sequence learning is what Keele, Ivry, Mayr, Hazeltine, and Heuer (2003) aimed to capture with a recent model. The authors propose two subsystems: A unidimensional system encompassing independent learning modules, each of which is assumed to operate on input from one dimension only, so that sequence learning on any dimension takes place regardless of redundancies in other dimensions. The term module denotes “a system that performs a class of computations and that can be interfaced with different inputs and outputs” (Keele & Curran, 1995; p. 199). In Keele et al.’s view the unidimensional modules extract regularities automatically, that is, even if that dimension is not attended to. Furthermore, a multidimensional system is assumed, which associates task-relevant stimuli from different dimensions provided that they are correlated and attended to.

The model, however, remains vague with regard to what exactly constitutes a dimension. As a first approximation, Keele et al. propose that different modalities may establish separate dimensions, but they note that stimulus attributes within a modality might also constitute dimensions.

In most of the experiments on independent learning of different sequences participants were presented with a response-correlated stimulus sequence (S&R) and a purely perceptual sequence (S), that is, a sequence of stimulus attributes which were not relevant for determining the required response (Deroost & Soetens, 2006a; Mayr, 1996; Riedel & Burton, 2006; Rüsseler, Münte, & Rösler, 2002). For example, on each trial in Mayr's (1996) Experiment 1, one of four objects was presented in one of four locations. Participants responded to the identity of the objects, which appeared in a repeating sequence (S&R). At the same time, the locations were determined by another repeating sequence (S). Because the two sequences differed in length, they were continuously shifted against each other and thus uncorrelated. At the end of the experiment, test blocks were implemented in which either only one of the sequences was replaced with a random sequence or both of them were randomized. Participants' RTs increased compared to adjacent regular blocks in all of these test blocks, but the RT increase was more pronounced when both sequences were randomized in the same test block than when only one of the sequences was randomized, indicating that the S&R sequence as well as the S sequence were learned independently of each other. Had the object or the location sequence not been learned, randomization of the respective sequence should not have incurred performance decrements relative to its presence. Furthermore, had a compound object-location sequence been learned instead of independent learning, randomizing either aspect of the compound sequence (object or location) would have been tantamount to randomizing the entire sequence, and performance decrements should not have differed between test blocks.

Subsequent experiments (Deroost & Soetens, 2006a; Riedel & Burton, 2006; Rüsseler et al., 2002) have replicated independent learning of an S&R sequence but have yielded no evidence in favor of independent learning of an uncorrelated S sequence. Thus, the evidence for independent learning of a response-irrelevant stimulus sequence implemented concurrently with an S&R sequence is inconsistent and presumably depends upon the amount of attention attracted by the response-irrelevant stimulus dimension (cf. Jiménez & Méndez, 1999; Schmidtke & Heuer, 1997, Experiment 3). Additionally, these findings are at odds with the assumption of unidimensional sequence learning modules which automatically register any redundancy in the order of stimuli or stimulus attributes, at least inasmuch as 'automatically' is understood to mean 'independent of attention'.

To the best of my knowledge, there are only two studies which have explored the issue of independent learning of two response-relevant stimulus (S&R) sequences (Frensch & Miner, 1995; Schmidtke & Heuer, 1997). Frensch and Miner (1995, Experiment 2) presented in each trial of an SRT task either one of two letters or one of two graphical symbols. Letters and symbols appeared alternating in a fixed 10-element sequence, so that there were two interwoven five-element sequences of letters and symbols, respectively. The assignment of stimuli to responses as shown at the bottom of the computer screen was randomly changed from one trial to the next. Consequently, letters and symbols were response-relevant, but neither sequence was correlated with a repeating sequence of responses. At the end of the experiment either the letter sequence or the symbol sequence was replaced with a random sequence. In the letter change group only RTs for letters and in the symbol change group only RTs for symbols increased, indicating independent learning of both sequences. Had there been integrated learning of the 10-element sequence of letters and symbols, replacing either one of these two interwoven sequences should have also slowed down responding to stimuli from the respective other sequence.

Schmidtke and Heuer (1997) used a dual-task SRT paradigm. Between the stimuli of an ordinary SRT task either a high-pitched or a low-pitched tone was inserted and participants were asked to press a foot pedal whenever a high-pitched tone appeared. In one of the conditions the order of the visual stimuli for the primary SRT task as well as the order of the tones for the secondary task followed a different fixed 6-element sequence. After some practice the two sequences were shifted relative to each other so that only regularities between them were altered whereas the within-sequence regularities remained unaffected (shift probe). Nevertheless, all responses were somewhat delayed indicating that participants had learned about the interrelations between both sequences, that is, integrated learning had taken place. In additional test blocks either one of the two stimulus sequences was replaced with a random sequence. In these random probes significant RT increases were observed for both tasks, even for that task for which the stimulus sequence remained intact. This finding also indicated integrated learning of the two sequences. However, as RTs increased more in the random probes than in the shift probes Keele et al. (2003; p. 323) concluded in their review of Schmidtke and Heuer’s experiments that besides integrated learning of the compound sequence the two sequences were also learned at least partly independently of each other.

Taken together, both studies provide evidence in favor of independent learning of two response-relevant stimulus sequences, thus supporting the notion of independent sequence learning modules. Frensch and Miner (1995) explicitly speculated that the letter and the symbol sequence might be acquired in different compartments of working memory (Baddeley & Hitch, 1974): the letter sequence in the phonological loop and the symbol sequence in the visuo-spatial sketch pad. In case of Schmidtke and Heuer's (1997) experiments various modules are also likely as the task involved not only two stimulus modalities but also two different effectors. Consequently, independent modules for visual and acoustic stimuli as well as for hand- and foot-movements are conceivable. Thus, besides confirming independent sequence learning, the study of Schmidtke and Heuer raises the question to what extent not only different types of stimuli but also different effectors may constitute independent learning modules. These two possibilities cannot be disentangled on the basis of Schmidtke and Heuer's experiments. Experiment 2 in the series of experiments reported here was designed in order to resolve this ambiguity.

Keele et al. (2003) explicitly speculated that "distinctions within the motor system (e.g., hands vs. feet) may also constitute dimensions" (p. 317). In essence, the existence and operation of unidimensional sequence learning modules for separate effectors would entail at least partly independent learning of effector-related sequences. Moreover, considering that Keele et al. envision "the input to each [unidimensional] module restricted to information along a single dimension" (p. 317) so that "each unidimensional module automatically extracts regularities in its input" (p. 317), sequence knowledge acquired via any such putative effector-based sequence learning modules will necessarily be represented in an effector-specific manner. Research relevant to the issue of effector specificity of sequencing skill is summarized next.

2.3 Effector Specificity of Sequence Learning

"Learning is said to be effector dependent to the extent that training of one set of muscles (e.g., those of the right hand) does not generalize to another (e.g., those of the left hand)" (Bird & Heyes, 2005; p. 262). The term effector-specific is also widely used instead of effector-dependent, and I will use both terms interchangeably.

The notion that procedural memory for sequential actions may be stored in a way which restricts their execution to the effector used during acquisition might appear implausible on principle when considering the relative inflexibility that would be inherent in such a system, especially when contrasted with an alternative architecture based on abstract representations of sequential actions which would readily support transfer between effectors. Indeed, there is ample evidence showing that animals and humans code movements in terms of an external reference frame (allocentric) rather than in terms of an anatomical or egocentric one (e.g., Schicke & Röder, 2006; Tolman, 1948; Wickens, 1938, 1943). Another frequently cited example for effector-independence, which may be more directly relevant here because it concerns the relatively rapid execution of movement sequences, is the observation that writing samples produced by the same person but with different effectors (such as the hand, the arm, the mouth) exhibit considerable similarities (Bernstein, 1947; Raibert, 1977; both cited in Keele et al., 1995; see also Merton, 1972). However, some dissimilarities emerge as well (e.g., Wright, 1990), for which it is unclear whether they merely reflect reduced effector competence (e.g., of the non-dominant hand) or whether they might reflect some effector-dependent sequence knowledge after all. The level of effector competence for realizing the transfer performance is most likely not an issue for relatively simple tasks such as key pressing. This makes the SRT task very suitable for investigating the representational nature of sequencing skill. Although a host of other findings from other paradigms could be cited in support of effector independence, I will focus in my review of investigations into the effector specificity of sequence knowledge primarily on investigations employing the SRT task, beginning with studies reporting effector independence of sequence knowledge before describing studies indicating that sequence knowledge is not always entirely effector-independent but that effector-specific components can also develop.

2.3.1 Evidence for Effector Independence in the SRT Task

A non-transferable component of sequence knowledge has failed to materialize in a number of experiments on the representational nature of sequence knowledge specifically aimed at investigating effector dependence or independence (see Table 1 for a summary).

For example, Keele et al. (1995) had participants respond to a sequence of spatial stimuli by pressing separate response keys in one of two response modes: Participants either pressed each key with a different finger of their dominant hand or they pressed all keys exclusively with the index finger of their dominant hand so that arm movements instead of finger movements were required. In a subsequent test phase some participants were transferred to the respectively other response mode. These participants expressed an equal amount of sequence knowledge as participants for whom the response mode did not change. In other words, the acquired sequence knowledge was still fully available despite the change of effector. Keele et al. obtained transfer – albeit not complete – even when participants switched from manual to verbal responding. Similar findings of perfect finger-to-arm transfer have also been reported by Grafton, Hazeltine, and Ivry (1998) as well as by Cohen et al. (1990, Exp. 2).

Table 1
Summary of SRT task studies indicating perfect transfer of sequence learning between different effectors.

Reference	Extent of practice	Sequence characteristics	Test of effector specificity
Keele et al. (1995)	160 sequence repetitions	5 elements; defined on 3 positions/keys	finger-to-arm / arm-to-finger transfer (Exp. 1 and 2); finger to vocal responding (Exp. 3); note: secondary tone-counting task in Exp. 2 & 3, but not in Exp. 1
Grafton et al. (1998)	98 sequence repetitions	6 elements; defined on 4 positions/keys	finger-to-arm transfer; note: secondary tone-counting task; fixed 1500 ms ISI$^+$
Cohen et al. (1990, Exp. 2)	200 sequence repetitions	5 elements; defined on 3 positions/keys	finger-to-arm transfer; note: secondary tone-counting task
Grafton et al. (2002)	132 sequence repetitions on average	6 elements; defined on 4 positions/keys	non-dominant-to-dominant-hand transfer; note: secondary tone-counting task; fixed 1500 ms ISI$^+$
Deroost et al. (2006)	approximately 250 and 100 sequence runs in Experiments 1 and 2 (1000 and 1200 trials of practice), respectively	probabilistic FOC* and SOC** sequence, respectively; defined on 4 positions/keys	dominant-to-non-dominant-hand transfer
Japikse et al. (2003)	1050 sequence repetitions	non-deterministic; 4 elements; defined on 4 positions/keys	dominant-to-non-dominant-hand transfer; note: sequence elements alternating with random elements
Willingham et al. (2000)	40 sequence repetitions	12 elements; defined on 4 positions	practice with crossed hands; transfer to responding with uncrossed hands

* FOC = first-order conditional sequence, ** SOC = second-order condition sequence (see section 2.1.1); $^+$ ISI = inter-stimulus interval.

Grafton, Hazeltine, and Ivry (2002) found excellent transfer of sequence knowledge from the non-dominant left hand to the dominant right hand. Deroost et al. (2006), who used probabilistic instead of deterministic sequences, also reported perfect intermanual transfer of sequence knowledge from the dominant right hand to the non-dominant left-hand when at test the sequence of stimuli and response locations remained unchanged relative to the practice phase. Similarly, Japikse, Negash, Howard, and Howard (2003) obtained complete transfer from the dominant right hand to the left hand after extensive practice of a particular kind of probabilistic sequence in which a random element (r) is inserted between any two sequence elements (e.g., ArDrBrCrArDrBrCr...).

An interesting additional aspect of studies of intermanual transfer of sequence learning is that, compared with responding to a random sequence, a performance benefit appears to be associated with responding to the mirrored sequence of stimuli so that the sequence of response locations was also mirrored (see also Wachs, Pascual-Leone, Grafman, & Hallet, 1994). Grafton et al. (2002) reported that in the transfer phase participants were faster to respond to the mirrored sequence of stimuli than to random stimuli, but not as fast as when responding to the original sequence. Deroost et al. (2006) even reported perfect transfer when the sequence of stimuli and response locations was mirrored; performance at test suffered only when participants had to respond to the mirrored sequence with the same hand they had already used during practice. Deroost et al. attributed this benefit for executing a sequence of finger movements homologous to the sequence of finger movements practiced with the other hand to sequence learning in terms of a schema of homologous fingers which is equally applicable to either hand. However, this conclusion is not consistent with Grafton et al.'s finding that mirror transfer was not complete, which they interpreted as reflecting that an additional transformation was required for mirror sequence execution. I will return to this issue below.

Also pertinent to the question of effector independence of sequence learning is an experiment by Willingham et al. (2000; Exp. 2). They had participants respond in a standard SRT task with crossed hands during practice but with uncrossed hands in a subsequent transfer phase. At test, the sequence of stimuli was either unchanged so that participants pressed the same sequence of keys as before but with a different sequence of finger movements, or the sequence of stimuli was altered in such a way that participants executed the same sequence of finger movements as during practice but thus pressing a different sequence of keys. Transfer was observed only in the former but not in the latter condition, indicating that sequence learning is “not represented as a particular set of muscle commands” (p. 367).

To summarize, the studies just reviewed consistently show that sequence knowledge is represented in a way that is independent of the effector used during acquisition. In other words, sequence knowledge appears to be abstract inasmuch as it is readily interfaced with different implementation systems. However, contrary evidence has accumulated in recent years, which indicates that under conditions of extensive practice sequencing skill can be partly effector-specific.

2.3.2 Evidence for Effector Specificity in the SRT Task and Other Sequencing Tasks

I will give an overview of these findings (see Table 2) before identifying the key procedural differences between these two sets of studies which might account for the ostensibly contradictory results. The overview begins with experiments in which manipulations of S-R mappings were employed in order to dissociate transferable and non-transferable components of sequence learning and then turns to veritable transfer experiments.

Jordan (1995) provided evidence suggesting that skill in performing extensively practiced sequential actions (e.g., typing) is not entirely effector-independent but relies in part on effector-specific representations. Specifically, he argued that effector-specific aspects of sequential skill most likely concern coarticulation, that is, the optimization of transitions between single actions in a sequence of actions, so that execution of a movement in the sequence might vary depending on the subsequent movement. Coarticulation is a common phenomenon in speech production (e.g., Kent & Minifie, 1977). In case of typing, coarticulation pertains to the optimization across more than a single keystroke. For typing, such optimization of coarticulation can only develop for words but not for non-words because typing typically involves words only. With this in mind, Jordan had skilled typists engage in a relearning task: They practiced for thousands of trials with an altered keyboard on which two pairs of adjacent letters were switched (*A* was switched with *S*, and *H* was switched with *J*). The task in the relearning phase was to execute a single key press in response to a single letter presented on the monitor. Thus, participants had the opportunity to relearn the separate actions of pressing a certain key for a certain letter, but could not adapt to the altered keyboard with regard to typing whole sequences of key presses (i.e., coarticulation). The critical dependent variable was participants' performance when copy-typing prose and nonsense text before and after relearning: Performance with the altered keyboard (after relearning) was worse than with a regular keyboard (before relearning) for both types of text. However, the decline was more pronounced for prose than for nonsense text. If typing skill did not rely at least in part on optimization of coarticulation and was completely effector-independent instead, the decline should have been the same for both types of text. Detailed analyses of typing errors after relearning support this conclusion and suggest that the strong version of effector independence of sequential skill in typing cannot be upheld. The role of effector-specific representations in skilled typing has also been demonstrated by Rieger (2004). Although her experiments were not immediately concerned with the sequencing aspect of skilled typing, results showed that letters automatically activate effector-specific representations of corresponding keypresses.

Bapi, Doya, and Harner (2000) also manipulated the mapping between stimuli, finger movements, and keys to be pressed. This strategy is reminiscent of Jordan's (1995) inasmuch as, instead of transferring participants to another effector, participants at test continue performing with the same effector but under a different mapping as during training. Bapi et al. had participants practice a sequence of 10 pairs of key presses on a 3x3 keypad with three fingers of the dominant right hand. Ten pairs of imperative stimuli (two lighted squares in a 3x3 matrix) appeared, with the time interval between successive pairs of imperative stimuli fixed at 1200 ms. During practice, participants had to determine and learn the order of key presses within each pair by trial and error (if participants were not fast enough, or pressed a wrong key, or pressed the right pair of keys in the wrong order, they had to start over). In test phases, after varying amounts of practice (early, intermediate, extensive), either the hand was rotated 90° while the keypad remained in place (so that the practiced sequence of keys had to be pressed with different finger movements), or both the hand and the keypad were rotated 90° (so that the practiced sequence of finger movements had to be executed). The total time to complete two successive runs of the sequence suffered in both testing conditions relative to the regular compatible arrangement. However, with increasing practice participants benefited more from the preservation of the sequence of finger movements than from the preservation of the sequence of key presses implicating the development of effector-specific sequence knowledge. Rotation of the keypad entailed that the mapping between imperative stimuli in the matrix and keys in the keypad was changed compared to the conditions during practice, whereas this was not the case when only the hand was rotated. It might be that this increased difficulty of mapping induced participants to rely more on the unchanged sequence of finger movements.

Further evidence for effector-specific components of sequence learning has also been obtained in veritable transfer studies as described next**.** Park and Shea (2003) investigated effector specificity in a task requiring participants to produce a very simple response sequence consisting of two force peaks of different amplitude in a particular temporal relation to one another. This sequence of two consecutive force pulses was to be produced with the extensor muscle group (i.e., triceps) of the dominant right arm. Participants completed either 200 or 800 trials during practice. Following a 24-h retention interval participants were tested at producing the consecutive force pulses (a) as practiced (i.e., with the extensor muscle group of the right arm), (b) with the same muscle group as practiced but on the contralateral side (i.e., with the extensor muscle group of the left arm), or (c) with a different set of muscles on the ipsilateral side (i.e., with the flexor muscle group of the right arm). Findings indicate that

Table 2
Summary of studies indicating a non-transferable, effector-specific component of sequence learning.

Reference	Extent of practice	Sequence characteristics	Test of effector specificity
Jordan (1995)	skilled typists	prose vs. nonsense text	relearning task on altered keyboard with two pairs of switched keys
Bapi, Doya, & Harner (2000)	tested after 7, 14, and 89 successful sequence completions [number of aborted erroneous attempts unavailable]	10x2 elements; defined on 9 positions/keys	rotation of hand only (preserves practiced sequence of key presses) vs. together with keypad (preserves practiced sequence of finger movements);
Park & Shea (2003)	200 vs. 800 sequence repetitions	simple sequence of two consecutive force pulses of different amplitude	contralateral transfer (left instead of right extensor muscle group) and ipsilateral transfer (right flexor instead of extensor muscle group)
Verwey & Wright (2004)	1060 sequence repetitions	5 elements; defined on 3 positions/keys	transfer between two hand configurations (responding with fingers of one hand vs. responding with fingers of both hands): discrete sequence production task; 0 ms RSI[+]
Park & Shea (2005; Exp. 2)	150 vs. 600 repetitions	16 elements, defined on 4 positions	intermanual transfer (dominant-to-non-dominant arm); continuous arm movement sequence
Verwey & Clegg (2005; Exp 1)	1240 sequence repetitions on average	10 elements; TOC* sequence; defined on 3 positions/keys	intermanual transfer (dominant-to-non-dominant hand as well as non-dominant-to-dominant hand)

* TOC = third-order conditional sequence (see section 2.1.1); [+] RSI = response-stimulus interval

(continued on next page)

Table 2 (continued)

Reference	Extent of practice[a]	Sequence characteristics	Test of effector specificity
Osman, Bird, & Heyes (2005)	128 observed sequence repetitions	8 elements; defined on 4 position/keys	intermanual transfer (dominant-to-non-dominant hand); note: observational sequence learning
Bird & Heyes (2005)	96 observed sequence repetitions	6 elements; defined on 6 positions/keys	transfer from responding with index, middle, ring fingers of both hands to responding with thumbs (Exp. 1 & 2) or with crossed hands (Exp. 3); note: observational sequence learning
Heyes & Foster (2002; Exp. 2)	112 observed sequence repetitions	6 elements; defined on 6 positions/keys	transfer to new S-R mapping; note: observational sequence learning

[a] Refers to extent of sequence exposure by way of observation in studies of observational sequence learning (Bird & Heyes, 2005; Heyes & Foster, 2002, Exp. 2; Osman, Bird, & Heyes, 2005).

response structure (in particular, relative timing of pulses) is readily transferred to new muscles groups both after little and after extensive practice. However, transfer was reduced for the scaling component of responding (in particular, absolute force of pulses) after extensive practice but not after little practice, leading Park and Shea to conclude that “some aspect of [what was stored about] the force-time scaling of the response [...] seemed to be specific to the limb used during practice” (p. 39). Park and Shea specifically noted that in tasks involving discrete key presses, response structure (in particular, timing) is more important than the scaling of response force, and they suggest that these particular task demands might render key pressing tasks, such as the SRT task, less susceptible to the development of effector-specific sequence knowledge.

Nevertheless, Verwey and Wright (2004) obtained an effector-specific component of sequence learning after extensive practice in a key pressing task, namely the discrete sequence production (DSP) task. Performing in a DSP task usually involves executing rather short sequences of key presses in response to imperative stimuli. With extensive practice, participants know which sequence to press based only on the first stimulus which, thus, comes to act as an imperative stimulus for the entire sequence. The DSP differs from the standard SRT task inasmuch as sequence repetitions are clearly separated in time. Verwey and Wright had participants practice distinct 5-element sequences in one of two hand configurations, either with fingers of the right hand or with two fingers of the left hand and one finger of the right hand. After an extensive training phase, participants were tested with both hand configurations. Execution of the practiced sequences was faster than execution of the new sequences not only with the practiced but also with the unpracticed hand configuration, thus indicating effector-independent sequence learning. However responding with the unpracticed hand configuration was not as swift as with the practiced hand configuration, thus demonstrating an effector-specific component of sequence learning.

Extending their previous work, Park and Shea (2005; Exp. 2) investigated effector independence in a task more similar to the standard SRT task, although it did not involve key pressing. Participants moved their lower right arm horizontally back and forth between 4 positions in a fixed 16-element sequence which was continuously repeated. Participants completed either 150 or 600 repetitions of this continuous movement sequence prior to transfer. Participants in the latter group continued improving their performance in terms of speed and fluidity of sequence execution throughout practice. At test, participants with little practice responded as quickly and variably with their unpracticed left arm as with their practiced right arm. In contrast, participants with extensive practice did not show complete transfer of sequence learning.

Finally, effector-specific sequence learning after extensive practice has been demonstrated in a standard SRT task by Verwey and Clegg (2005). Participants in their Experiment 1 were significantly faster when responding with the transfer hand to the practiced sequence than when responding to a new unpracticed sequence, thus showing considerable intermanual transfer. However, responding with the transfer hand to the practiced sequence was not as fast as with the practiced hand, thus indicating a non-transferable component of sequence knowledge. In their Experiment 2, Verwey and Clegg compared sequence practice involving fingers of one hand with sequence practice involving fingers of both hands. Both one-handed and two-handed practice resulted in significant sequence learning. However, switching from one-handed to two-handed sequence execution did not incur significant costs in response speed, whereas one-handed sequence execution was significantly slower than two-handed sequence execution after two-handed practice. Based on this observation Verwey and Clegg concluded that effector-specific sequence learning consists of adjustments of sequence production to the biomechanical properties of the effector used. In essence, this is the equivalent of the development of coarticulation, that is, the optimization of transitions between single finger movements in a sequence of finger movements. Verwey and Clegg argue that such optimization plays a larger role for one-handed sequence execution than for two-handed sequence execution because biomechanical interactions among fingers of one hand are more severe than between hands.

Verwey and Clegg (2005) also tested participants on the mirrored version of the practiced sequence and found that responding with the unpracticed hand was faster to the mirrored sequence than to an unpracticed sequence (cf. Grafton et al., 2002; Deroost et al., 2006). However, in contrast to Deroost et al.'s (2006) findings, this mirrored sequence benefit was also apparent for the practiced hand, thus casting doubts on Deroost et al.'s conclusion that the mirrored sequence benefit is due to sequence knowledge being represented in terms of finger movements in such a way that it can be transferred to the homologous fingers of the other hand. Instead, it appears that mirror transfer might be based on an abstract effector-independent representation which requires additional transformations to be used for execution with either hand.

Also relevant in this context is a study by Kami et al. (1995; see also Karni et al., 1998), who had participants engage in extensive 5-week practice of a short sequence in a simple speeded finger-to-thumb opposition task. Participants performed the task with their non-dominant hand. The task involved bringing together the tip of the thumb with the tips of the index, middle, ring, or little fingers in a particular order (e.g., thumb–little, thumb–index, thumb–ring, thumb–middle, thumb–little). The relatively crude performance rate measure (number of sequence completions in a 30 sec interval) showed considerable improvements across the 5 weeks. These improvements did not generalize to an unpracticed sequence involving the same component finger-thumb opposition movements suggesting that benefits resulting from practice concerned the sequencing of these component movements, that is, the optimization of coarticulation. Furthermore, there was no significant transfer to the contralateral hand, although performing the practiced sequence with the contralateral hand involved executing the same sequence of homologous finger movements as practiced with the other hand.[2] This finding casts further doubts on the validity of the notion that sequence knowledge might be represented in terms of homologous fingers.

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[2] The finger-thumb opposition task fundamentally differs from the tasks discussed so far inasmuch as it involves little if any external stimulation (e.g., imperative stimuli, exteroceptive response effects) or goals (e.g., keys to be pressed). Instead the movement itself is the goal, and unless participants watch their own hand as they perform the task, there are only efferent motor commands and proprioceptive feedback available for sequence learning mechanisms to operate on. Therefore, the finger-thumb opposition task might be particularly susceptible to the development of an effector-specific, non-transferable sequence representation.

2.3.3 Reconciling Conflicting Findings Regarding the Effector Specificity of Sequence Knowledge

To summarize, an effector-specific component of sequence knowledge has been repeatedly demonstrated in a range of different sequencing tasks, and in all of these studies its emergence has been framed in terms of coarticulation. Typically, an effector-specific component of sequence knowledge appears to develop only as a result of extensive practice, whereas studies reporting effector independence usually involved considerably less practice. There seems to be one exception to this generalization: Japikse et al. (2003) found near-perfect intermanual transfer although their participants engaged in more than 1000 sequence repetitions during practice. However, Japikse et al. used a setup in which only every other stimulus appeared according to a fixed sequence while each intermittent stimulus was chosen randomly, and participants responded both to sequence stimuli and to random stimuli with the same fingers on the same keys. Therefore, in terms of executed finger movements, the resulting sequence was essentially non-deterministic, so that there were no regularly reoccurring consistent patterns of finger movements for which coarticulatory optimization could have developed. It is not surprising, then, that no effector-specific sequence knowledge developed. Thus, the key conditions amenable to the development of effector-specific sequence knowledge may be best characterized as extensive practice of the same deterministic sequence of movements.

Under particular conditions, however, effector-specific sequence learning has been found after relatively little exposure to the sequence. Osman, Bird, and Heyes (2005) reported the acquisition of effector-specific sequence knowledge by observation: Participants watched a video of someone’s right hand responding in an SRT task and completing 128 repetitions of an 8-element sequence. Subsequently, the observers performed in an SRT task. When using their dominant right hand, responding to the observed sequence was faster than responding to the reversed sequence, indicating learning of the observed sequence. However, no such difference in performance between responding to the observed and the reversed sequence was obtained when participants used their left hand, indicating that no intermanual transfer of sequence learning occurred. Additional evidence for effector-specific sequence learning by observation has been obtained by Bird and Heyes (2005; see also Heyes & Foster, 2002). Notably, observational sequence learning in these experiments was not only effector-specific but also explicit, which is at odds with the notion that effector-specific sequence knowledge is predominantly implicit, whereas effector-independent sequence knowledge is usually explicit (Hikosaka, Nakamura, Sakai, & Nakahara, 2002; see also Rüsseler & Rösler, 2000).

Heyes and colleagues interpret their findings in reference to research into the human “mirror system” (e.g., Aziz-Zadeh, Maeda, Zaidel, Mazziotta, &, Iacoboni, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Rizzolatti, Fogassi, & Gallese, 2001) which shows that execution and observation of actions engender comparable patterns of neural activation. In light of this, it is conceivable that “movement observation may substitute for movement execution in effector-specific sequence learning” (Heyes & Foster, 2002; p. 594) and thus that “practice and observation mediate skill development through the very same processes of motor learning” (Osman et al., 2005; p. 26).

Bird and Heyes (2005; see also Osman et al., 2005) argue that their finding of effector-specific sequence learning is reconcilable with the notion that effector specificity develops with increasing practice. They point out that, whereas they used very simple sequences with unique transitions, studies showing effector-independent sequence learning (see Table 1) have used more complex sequences and some even included a secondary tone-counting task to distract attention from the sequence in the primary SRT task. Based on this, they suggest that sequence learning might have been more advanced in their experiments than in the other experiments after a comparable amount of practice (observation).

There is one additional study to be discussed which seems difficult to reconcile with the notion that effector specificity develops only with considerable sequence practice. Palmer and Meyer (2000) had experienced adult pianists and relatively inexperienced child pianists play simple 12-note melodies with fingers of one hand as quickly as possible on a computer-monitored piano. Participants practiced a melody 10 times before performing one of four transfer sequences. The transfer sequences were constructed so that (a) either the practiced melody or a different melody was played, and (b) playing required either the practiced sequence of fingers movements to be executed with the practiced hand or a different sequence of finger movements to be executed with the other hand. These two factors were fully crossed. Skilled adult pianists showed better transfer when the melody was retained from training to transfer than when it was changed irrespective of the hand and finger movements involved, indicating that their representation of the musical sequence was abstracted from the particular effectors used during practice. In contrast, novice child pianists showed complete transfer only when both the melody and the sequence of finger movements were retained from training to transfer. Their transfer performance suffered not only when playing a different melody with the same sequence of finger movements but also when playing the same melody with a different sequence of finger movements. Thus, their representation of the sequence appears to rely on the particular movements involved as well as on the abstract pitch relationships.

The fact that effector independence was observed in adult pianists is not very surprising: Although highly skilled at piano playing in general, they had very little practice with the particular sequences tested and thus little opportunity to develop coarticulatory optimization for those sequences. But why did child pianists' show an effector-specific component of sequence learning? One reason for this might be that child pianists have not yet mastered the independent control of fingers of one hand to the same extent as adult pianists and therefore need to concentrate more on which finger to move next. In other words, child pianists might need to conceptualize the task more in terms of moving certain fingers, and as a consequence might learn the sequences more in terms of particular finger movements. In contrast, for expert pianists it has been shown that movement control in piano playing occurs at an abstract level relying fundamentally on acquired action-effect associations so that the anticipation of abstract action effects (e.g., the sound produced by hitting a key on the piano) induces the corresponding actions (Drost, Rieger, Brass, Gunter, & Prinz, 2005a, 2005b).

2.4 Goals of the Present Research

As we have seen, the question of independent learning of effector-related sequences has not yet been investigated systematically (see section 2.2). The related issue of effector-specific sequence learning has received considerably more attention (see section 2.3) and research has shown that effector-specific representations of sequence knowledge can indeed develop, usually as a result of extensive practice. However, none of these latter studies have addressed concurrent effector-specific learning with multiple effectors.

The main goal of the present research was to fill that gap by investigating independent learning of hand-related action sequences, that is, two sequences responded to in parallel in an SRT task, one with the left and the other with the right hand. As my interest was with highly skilled action sequences, the experiments involved extensive practice. Although the SRT task has been used frequently to investigate implicit learning, its use in the present research was motivated by the goal to investigate sensory and motor contributions to highly skilled sequential behavior, and not by a concern with implicit versus explicit learning. Nevertheless, assessments of participants' explicit sequence knowledge have been included in all experiments and results will be reported briefly in the respective results sections for the interested reader.

Beyond the general question of whether independent learning of hand-related sequences occurs at all (Experiments 1, 2, 3, 4), the research focused particularly on the nature of the memory representations underlying independent learning of hand-related sequences:

- The contributions of sensory and motor information to independent learning of effector-related sequences were disentangled by manipulating and eventually eliminating any perceptual basis for separate S-S and R-S learning of the two sequences (Experiments 2, 3, 4) so that any independent learning of hand-related sequences can only be ascribed to separate R-R learning for each hand.
- Additionally, tests of intermanual transfer were implemented (Experiments 1, 2, 3, 4) to assess whether independently acquired sequence knowledge was effector-specific or effector-independent.

The strategy of eliminating any perceptual basis for independent learning of hand-related sequences in order to isolate purely motor-based independent learning was complemented by a strategy of creating increasingly unfavorable conditions for obtaining motor-based independent learning in order to assess its robustness. To this end, the occurrence of independent learning of effector-related sequences was tested …

- not only under conditions of simultaneous stimulus presentation and responding (Experiments 1 and 2) but also under conditions of alternating stimulus presentation and responding (Experiment 3 and 4) so that the stimuli/responses belonging to a hand-related sequence are separated by intervening stimuli/responses belonging to the other hand-related sequence, which might favor integrated sequence learning.
- not only for hand-related sequences of different length (Experiments 1, 2, 3), which entails that the two sequences are largely uncorrelated, but also for hand-related sequences of the same length (Experiment 4) so that the two sequences are highly correlated as is probably more representative of everyday multi-effector sequential actions and which might favor the acquisition of integrated sequence learning as well.
- under conditions of responding to sequence stimuli appearing alternately with random stimuli; in this situation, the supposed existence and operation of separate sequence learning modules for each hand (cf. Keele et al., 2003; p. 317) should express itself in a benefit for learning the sequence when the assignment is such that responding to sequence stimuli involves only fingers of one hand compared to when the assignment is such that responding to sequence stimuli involves fingers of both hands (Experiment 5).

Finally, the acquisition of effector-specific sequence knowledge was investigated under conditions of unimanual responding arranged to be maximally conducive to complete intermanual transfer of acquired sequence knowledge as participants responded to the same sequence of identical spatial stimuli by pressing the same keys with homologous fingers of the practiced and the transfer hand (Experiments 6 and 7). Therefore, incomplete intermanual transfer under these conditions can only be ascribed to the existence of hand-specific sequence knowledge. Experiment 6, in particular, was designed to allow a fine-grained analysis of the time course of the development of effector-specific sequence knowledge.

3 Experiments 1 & 2: Simultaneous Bimanual-Bisequential SRT Task

Experiments 1 and 2 were designed to investigate to what extent and under which conditions two simultaneously performed uncorrelated sequences of stimuli/responses are learned independently of one another. Experiment 2 in particular was aimed at determining the extent to which any acquired independent sequence knowledge is based (a) on representations relying on stimuli, that is, on sequence knowledge of perceptual origin which is transferable between effectors, or (b) on representations of effector-specific movements, that is, on non-transferable knowledge about response sequences.

3.1 Experiment 1

Participants practiced a repeating sequence of bimanual key presses. On each trial two imperative stimuli appeared simultaneously, one for each hand, and participants were instructed to respond as simultaneously as possible with the appropriate fingers (for a similar procedure, see van der Graaf, de Jong, Maguire, Meiners, & Leenders, 2004). There was a fixed repeating sequence for the fingers of the left hand and another uncorrelated repeating sequence for the fingers of the right hand. Together these two hand-related sequences established a complex repeating compound sequence. This setting imitates requirements of coordinated hand movements in response to different environmental aspects.

Following extensive practice, three different types of test blocks were introduced: First, only one of the two hand-related sequences was replaced with a pseudo-random sequence. Second, both hand-related sequences were abolished, that is, both hands responded to a random sequence. Finally, transfer blocks were implemented in which the sequence practiced with the left hand was transferred to the right hand and vice versa.

In order to assess the amount of independent and integrated sequence learning, errors and RTs were evaluated. Errors were calculated for each hand separately whereas mean RTs were calculated for both hands together. As participants were instructed to execute the two responses simultaneously, a delay in responding with one hand will also delay the response with the other hand so that separately analyzing the RTs of each hand does not make sense.

Assuming that on each trial the two required responses are selected more or less sequentially, the following data pattern would indicate independent learning of the two sequences: Abolishing only one of the two sequences should result in a selective increase of errors in the respective hand and an increase of mean RTs, whereas abolishing both sequences should cause an increase of errors in both hands and a more pronounced increase of mean RTs. In contrast, integrated learning of the compound sequence would be indicated by an equal increase of errors and RTs for both hands irrespective of whether the sequence of either of the hands or of both hands is abolished.

Furthermore, in case of independent learning, the amount of intermanual transfer can be assessed by the performance in transfer blocks. Better performance in transfer blocks compared to performance in test blocks in which both of the sequences are abolished would show that responding to a random sequence with one hand and to a transferred sequence with the other hand (i.e., a practiced sequence carried out with the 'unpracticed' hand) is easier than responding to two random sequences. Such an advantage would suggest that at least part of the sequence knowledge has been transferred from the practiced to the 'unpracticed' hand. If, however, performance in transfer blocks equals performance with two random sequences, hand-related but non-transferable sequence knowledge is implicated.

3.1.1 Method

Participants. Twenty-four individuals (mean age 22.5 years) volunteered to participate in Experiment 1 either in partial fulfillment of course requirements or for a payment of €15. Twenty participants reported to be predominantly right-handed, the remaining four asserted to be predominantly left-handed. Participants' handedness was assessed in a post-experimental interview. They were asked to indicate for each of the following tasks with which hand they typically perform it (left hand, right hand, both hands): painting/drawing, throwing a ball at a target, using an eraser, dealing cards (the hand not holding the deck).

Task and Design. The presence or absence of the fixed sequences constituted the within-subjects factor. In particular, the following types of test blocks were implemented (see also Table 3)[3]: First, the fixed sequence participants had practiced with their left hand was replaced with a pseudo-random sequence while the right-hand sequence was retained (test block L_{rand}). Second, the sequence participants had practiced with their right hand was replaced with a pseudo-random sequence while the left-hand sequence was retained (R_{rand}). Third, both fixed sequences were replaced with pseudo-random sequences in the same test block (LR_{rand}).

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[3] For a better understanding of the names chosen for the different types of test blocks, keep in mind the following naming convention: The capital letters (L or R) in test block names refer to the sequence practiced with the respective hand (left or right) during acquisition; they do not refer to the hand itself. The subscript ($_{rand}$ or $_{trans}$) denotes in which way the sequence indicated by the capital letter has been manipulated. For example, L_{rand} means that the sequence practiced with the left hand is replaced by a random sequence; of course, this is tantamount to the left hand receiving a random sequence. The importance of the distinction will become clearer when looking at another example: According to the naming convention, L_{trans} means that the sequence practiced with the left hand is transferred (to the right hand); it does not mean that the left hand receives (by way of intermanual transfer) the sequence practiced with the other (right) hand.

In addition to that, there were test blocks in which, fourth, the sequence practiced with the left hand was transferred to the right hand while a pseudo-random sequence was presented for the left hand (L_{trans}), and, fifth, the sequence practiced with the right hand was transferred to the left hand while a pseudo-random sequence was presented for the right hand (R_{trans}). The sequences were transferred from the practiced to the unpracticed hand in such a way that the left-to-right ordering of stimulus (and key) locations was maintained, that is, the sequences were not mirrored.

Table 3
Assignment of fixed sequences and pseudo-random sequences to the left and the right hand in regular blocks and in the different types of test blocks.

Block type	Sequence	
	Left hand	Right hand
Regular block	practiced left	practiced right
Test block		
L_{rand}	random	practiced right
R_{rand}	practiced left	random
LR_{rand}	random	random
L_{trans}	random	practiced left
R_{trans}	practiced right	random

Apparatus and Materials. Stimulus presentation and response registration was controlled by the E-Prime software package (Schneider, Eschman, & Zuccolotto, 2002). Participants used a standard QWERTZ keyboard for responding. Stimuli were presented to participants on a 17-inch computer monitor. Responses and RTs were recorded separately for the left and the right hand.

The imperative stimuli were asterisks 5 mm in diameter presented in black on a white background. Asterisks could appear in any one of six horizontally aligned locations on the screen, each of which was marked by a horizontal line 8 mm in length also appearing in black. The asterisks were presented centered above these lines. The lines (locations) were arranged in two groups of three with a distance of 45 mm between the groups. Within each group the lines were 6 mm apart.

The six keys S, D, F, J, K, and L on the keyboard served as response keys and were assigned from left to right to the six lines (locations) on the screen. The response keys in turn were assigned from left to right to the ring, middle, and index finger of the left hand and the index, middle, and ring finger of the right hand.

Two imperative stimuli appeared simultaneously on every trial: one stimulus in one of the locations on the left-hand side (referred to here as 1, 2, 3, from left to right), and another stimulus in one of the locations on the right-hand side (also referred to here as 1, 2, 3, from left to right). During training, the left-hand stimuli followed a repeating sequence independently of the right-hand stimuli, which followed another repeating sequence.

A 5-element sequence (32121) and a 6-element sequence (121323) were used. The 6-element sequence is a second-order conditional sequence. The 5-element sequence contains two unique transitions (3-2 and 2-1) and two third-order conditional transition (321-2 and 121-3). Because the two sequences are of different length, they are uncorrelated and establish a common dual-stimulus sequence which repeats every 30 trials. The structure of this compound sequence can be characterized in terms of transition probabilities as follows: Each of the 9 possible stimulus pairs has at least 2 possible successor pairs. Among the 24 occurring combinations of two consecutive stimulus pairs (2-tuples) there are 18 with unique successors and 6 with two potential successors. Only at the level of 3-tuples is the compound sequence fully predictable as there is only one possible successor for each 3-tuple. So the compound sequence is a hybrid sequence containing both unique first-order and unique second-order conditional transitions.

Pseudo-random sequences were 90 elements long so that each matched the length of an entire test block. Furthermore, they were constructed to resemble the fixed sequences which they replaced in that stimuli appeared with the same frequency and did not repeat on consecutive trials. From a large set of such pseudo-random sequences as many were selected as there were test blocks in the experiment under the constraint that the selected pseudo-random sequences shared as few triples as possible with the to-be-replaced fixed sequence. Specifically, out of the total of 88 triples (3-tuples) contained in each of those pseudo-random sequences selected to replace the 5-element sequence (triples wrapping around from the last to the first elements in a 90-element pseudo-random sequence were not counted because no such wrap-around occurred in the test blocks), either 45 or 46 triples matched one of the 5 triples contained in the 5-element sequence. Similarly, each of those pseudo-random sequences replacing the 6-element sequence contained between 29 and 32 triples (out of a total of 88) matching one of the 6 triples in the 6-element sequence. The same pseudo-random sequences were used for each participant.

Procedure. Participants were tested individually. Half of the participants practiced the 5-element sequence with the left hand and the 6-element sequence with the right hand, while the assignment was reversed for the remaining participants.

The experiment was conducted in three sessions scheduled for different days with a maximum of one day between any two consecutive sessions. Session 1 started with a warm-up block in which pseudo-random sequences were presented for both hands, followed by ten fixed-sequence blocks. Session 2 comprised 15 blocks, the first seven of which were fixed-sequence blocks. Beginning with the eighth block (i.e., after 408 repetitions of the 5-element sequence and 340 repetitions of the 6-element sequence), four test blocks alternated with four fixed-sequence blocks. The four test blocks were: one L_{rand}, one R_{rand}, and two LR_{rand}. The order of these test blocks was counterbalanced across participants with the pair of LR_{rand} test blocks being treated as one entity. Session 3 started with five fixed-sequence blocks, and beginning with the sixth block (i.e., after a total of 624 repetitions of the 5-element sequence and 520 repetitions of the 6-element sequence, not counting sequence repetitions in session 2 L_{rand} and R_{rand} test blocks), four test blocks alternated with four fixed-sequence blocks as described for session 2. The order of presentation of these test blocks was also counterbalanced across participants with the additional constraint that no participant received the same ordering of test blocks as in session 2. Finally, blocks 14 and 15 were test blocks of the L_{trans} and R_{trans} type. The order in which these transfer blocks appeared was counterbalanced across participants independently of the counterbalancing of the first four test blocks. The session concluded with a final fixed-sequence block.

Each fixed-sequence block comprised 120 trials, the warm-up block and all of the test blocks comprised 90 trials each. Each fixed-sequence block began at a different position in the compound 30-element sequence established by the two hand-related sequences. Each trial began with the simultaneous presentation of two imperative stimuli. As soon as the participant had executed two responses the next stimuli were presented. A response-stimulus interval (RSI) of 0 ms was primarily chosen in order to optimize conditions for the acquisition of effector-specific sequence knowledge. It has been suggested that the absence of an RSI may be advantageous for effector-specific learning (Verwey & Wright, 2004), although it certainly is not a necessary condition as demonstrated by Verwey and Clegg’s (2005) finding of effector-specific learning at an RSI of 200 ms. Additionally, the absence of an RSI may have resulted in limited explicit learning (cf. Destrebecqz & Cleeremans, 2001). When one or both of the participant’s responses were incorrect the German word for error (“Fehler”) flashed briefly (for 27 ms; 2 refresh cycles of the monitor) in red color below the row of location lines.

Prior to session 1, participants received written instructions presented on the screen. Participants were informed about the assignment of locations on the screen to keys on the keyboard and to fingers of the two hands as described above. Participants were told that two asterisks would appear in two of the locations in every trial, indicating which pair of keys to press. No mention was made of sequences. Both speed and accuracy were stressed in the instructions. Furthermore, participants were instructed to perform the two responses in each trial as simultaneously as possible. Instructions were repeated prior to the start of sessions 2 and 3. In each session participants took self-terminated rest periods between blocks during which a text on the screen reminded the participants of the requirements regarding speed and accuracy as well as the synchrony of the responses. The participants initiated each block by pressing the space bar.

After completing the SRT task in session 3, participants were debriefed about the presence and the exact length of the two sequences and were asked to recall both of them in full length, beginning with the sequence they had practiced with the left hand. More specifically, participants were asked to write down either the sequence of key presses or the sequence of stimuli and they were encouraged to guess if they could not recall parts of a sequence. They were also told that they could use their hands during recall and start at any position in the sequence.

3.1.2 Results

In order to focus presentation of results, only data from session 3 will be presented in detail. Session 2 data yielded largely the same results.

RTs from error trials (at least one incorrect response) were excluded from analysis (7.6%), as were outlier RTs (3 *SD* above or below the z-transformed mean RT as determined separately for every participant, every block, and every hand; 1.7%). Furthermore, RTs from those trials were excluded in which RTs for the left and right hand differed by more than 100 ms (2.0%). For the remaining trials the RTs of the left and the right hand were averaged. From these mean bimanual RTs for each trial the median RT was computed for every block. The means of the individual median RTs are shown in Figure 2. For each block, error rates were computed separately for both hands. The two test blocks of the type LR_{rand} were treated as a single test block.

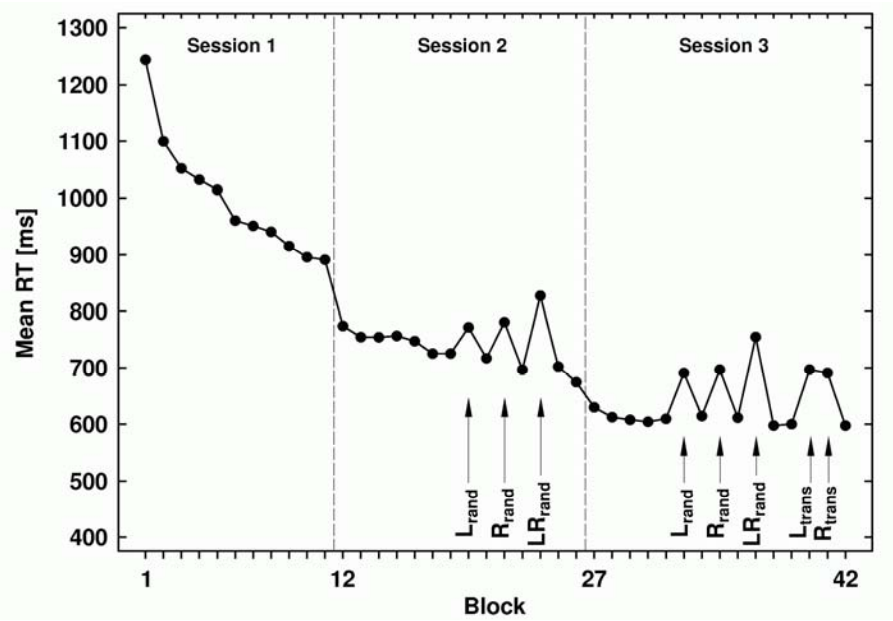


Figure 2. Means of individual median RTs in Experiment 1. For presentation purposes, test blocks are ordered in a consistent manner; in reality, the order of test blocks was counterbalanced across participants. Also, both for session 2 and session 3, data from the two LR_{rand} test blocks were combined into a single test block here. This is why there is no block 25 and no block 38 in this figure.

RT costs as an index of sequence learning were computed as the difference between the median RT in a test block and the mean of the median RTs in baseline blocks. For test blocks L_{rand}, R_{rand}, and LR_{rand} the baseline blocks were defined as the regular block preceding the first of these test blocks and the regular block following the last of these test blocks as well as those regular blocks in between (i.e., blocks 31, 33, 35, 37, and 39). For test blocks L_{trans} and R_{trans} the baseline blocks were the regular blocks adjacent to these test blocks (i.e., blocks 39 and 42). Error costs were computed in a manner analogous to RT costs. Error costs were obviously very small proportions, which raises the issue of whether parametric statistical analyses are appropriate for error cost data. Yet, none of the error costs variables differed significantly from a normal distribution, all Kolmogorov-Smirnov *Z*s between 0.345 and 1.171, all $p > .128$. Therefore, the data were analyzed with the more powerful parametric procedures instead of non-parametric statistical tests.

Whenever necessary, the degrees of freedom in repeated-measures analyses of variance (ANOVA) were adjusted with the Greenhouse-Geisser epsilon (ε_{GG}) in order to correct for any significant violations (Mauchly test) of the sphericity assumption. If a correction has been carried out, the unadjusted degrees of freedom are reported together with the respective ε_{GG}, and the corresponding reported *p*-values reflect the adjusted degrees of freedom. For each family of pairwise comparisons (paired-samples t-tests) *p*-values were subjected to the Bonferroni adjustment.

There were significant RT costs in every test block, all $t(23) > 7.44$, all $p \leq .001$. For relevant RT cost means and error cost means see Figure 3A.

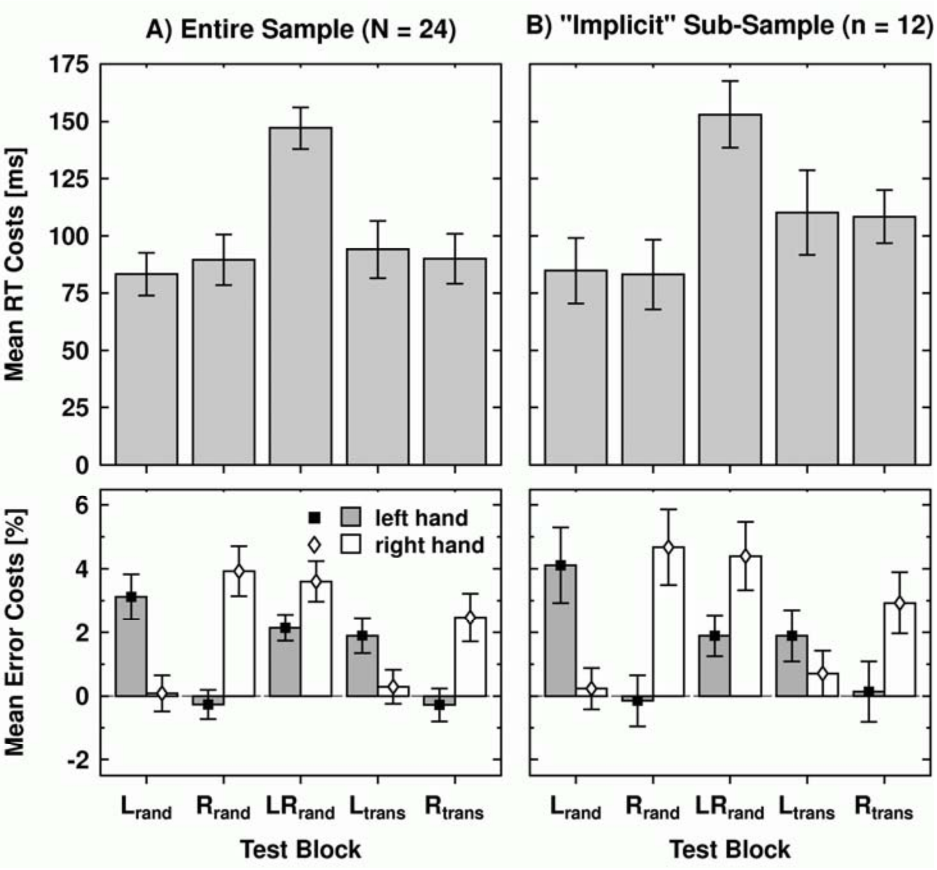


Figure 3. Mean RT and error costs in each of the test blocks in session 3 of Experiment 1 separately for the entire sample (A) and for the sub-sample of participants who possessed only fragmentary explicit knowledge about the sequences (B). Error bars represent standard errors of the means.

Randomization Probes: RT Costs. An ANOVA on session 3 RT costs with repeated measures on the factor Test Block (L_{rand}, R_{rand}, LR_{rand}) revealed a significant main effect, $F(2, 46) = 25.16$, $p \leq .001$, $\eta_p^2 = .522$, reflecting that RT costs (a) did not differ significantly between test blocks in which only one sequence was randomized while the other was retained (L_{rand} and R_{rand}), $t(23) = 0.61$, but (b) were smaller in those test blocks than when both sequences were randomized (test block LR_{rand}), both $t(23) > 5.37$, both $p \leq .001$. This pattern of RT costs could have also resulted if each participant had learned only one of the hand-related sequences but not the other: If that was the case (a) all participants would have had RT costs in test block LR_{rand}, and (b) lower RT costs in test blocks L_{rand} and R_{rand} would have resulted from averaging across participants with RT costs in only one of these test blocks but not the other. However, the correlation between the individual RT costs in test blocks L_{rand} and R_{rand} was positive $r(24) = .49$, $p \leq .016$, indicating that there was no such trade-off between learning of the left-hand sequence and learning of the right-hand sequence. Such a trade-off can also be ruled out based on the pattern of error costs as described next.

Randomization Probes: Error Costs. An ANOVA on session 3 error costs with repeated measures on the factors Hand (left, right) and Test Block (L_{rand}, R_{rand}, LR_{rand}) revealed a significant main effect Test Block, $F(2, 46) = 5.89$, $p \leq .01$, $\eta_p^2 = .204$, indicating generally higher error costs in test block LR_{rand} (2.9 %) than in test blocks L_{rand} (1.6 %) and R_{rand} (1.8 %), both $t(23) > 3.02$, both $p \leq .05$, between which error costs did not differ significantly, $t(23) = 0.52$. The main effect Hand was not significant, $F(1, 23) = 2.68$, $p \leq .115$, $\eta_p^2 = .105$, but the critical interaction between the factors Hand and Test Block was significant, $F(2, 46) = 20.34$, $p \leq .001$, $\eta_p^2 = .469$, $\varepsilon_{GG} = .743$.

In order to unpack this interaction, separate ANOVAs on error costs with repeated measures on the factor Test Block were computed for the left and the right hand. Both of these analyses revealed a significant main effect Test Block, both $F(2, 46) > 15.37$, both $p \leq .001$, both $\eta_p^2 > .400$, both $\varepsilon_{GG} < .824$. Significant right-hand error costs were evident in test blocks R_{rand} and LR_{rand}, both $t(23) > 4.98$, both $p \leq .001$, between which error costs did not differ significantly, $t(23) = 0.54$. Right-hand error costs were, however, significantly higher in those test blocks than in test block L_{rand}, both $t(23) > 4.09$, both $p \leq .001$, in which right-hand error costs were not significant, $t(23) = 0.15$. Significant left-hand error costs were evident in test blocks L_{rand} and LR_{rand}, both $t(23) > 4.40$, both $p \leq .001$, between which error costs did not differ significantly, $t(23) = 1.63$. Left-hand error costs were, however, significantly higher in those test blocks than in test block R_{rand}, both $t(23) > 4.62$, both $p \leq .001$, in which left-hand error costs were not significant, $t(23) = -0.58$. In other words, performance suffered only for that hand which lost its sequence while performance with the other hand, which retained its sequence, was unaffected.

Transfer Probes: RT Costs. An ANOVA on session 3 RT costs with repeated measures on the factor Transfer Block (LR_{rand}, L_{trans}, R_{trans}) revealed a significant main effect, $F(2, 46) = 27.00$, $p \leq .001$, $\eta_p^2 = .487$, indicating increased RT costs in LR_{rand} test blocks compared to both the L_{trans} and the R_{trans} test block, both $t(23) > 6.32$, both $p \leq .001$, between which RT costs did not differ significantly, $t(23) = 0.45$.

Transfer blocks were somewhat more regular than the LR_{rand} block: For any given trial in transfer blocks L_{trans} and R_{trans} there are only two possible subsequent stimulus combinations (i.e., pairs consisting of one left-hand and one right-hand stimulus) because for the hand with which participants respond to the transferred sequence the position of the next stimulus is fixed, and for the other hand there are only two possible subsequent stimulus positions as there were no immediate repetitions of the same stimulus position on consecutive trials. In test blocks LR_{rand} in contrast, there are four possible subsequent stimulus combinations for any given trial because immediate repetitions are avoided independently for both hands so that for each hand there are two possible subsequent stimulus positions and, thus, four possible stimulus pairs.

Given the higher regularity in transfer blocks than in test block LR_{rand}, the reduced costs in the transfer blocks might be due to within-block learning. In order to explore this possibility an analysis including Block Half (first vs. second) as an additional within-subjects factor was computed. However, the critical Transfer Block × Block Half interaction was not significant, $F(2, 46) = 0.89$, $\eta_p^2 = .037$. Moreover, higher RT costs in test block LR_{rand} than in transfer blocks L_{trans} and R_{trans}, both $t(23) > 4.84$, both $p \leq .001$, were already evident in the first block half, $F(2, 46) = 14.62$, $p \leq .001$, $\eta_p^2 = .389$. In sum, performance suffered less when executing the transferred sequence together with a pseudo-random sequence than when executing two pseudo-random sequences indicating intermanual transfer.

Transfer Probes: Error Costs. An ANOVA on session 3 error costs with repeated measures on the factors Hand (left, right) and Transfer Block (LR_{rand}, L_{trans}, R_{trans}) revealed a significant main effect Transfer Block, $F(2, 46) = 8.11$, $p \leq .005$, $\eta_p^2 = .261$, $\varepsilon_{GG} = .789$, indicating generally higher error costs in test block LR_{rand} (2.9 %) than in test blocks L_{trans} (1.1 %) and R_{trans} (1.1 %), both $t(23) > 3.48$, both $p \leq .01$, between which error costs did not differ significantly, $t(23) < 0.01$. The main effect Hand was not significant, $F(1, 23) = 2.63$, $p \leq .118$, $\eta_p^2 = .103$, but the critical interaction between the factors Hand and Transfer Block was significant, $F(2, 46) = 11.04$, $p \leq .001$, $\eta_p^2 = .324$.

In order to unpack this interaction, separate ANOVAs on error costs with repeated measures on the factor Transfer Block were computed for the left and the right hand. Both of these ANOVAs yielded a significant main effect Transfer Block, both $F(2, 46) > 7.12$, both $p \leq .01$, both $\eta_p^2 > .236$. Significant right-hand error costs were evident in test blocks LR_{rand} and R_{trans}, both $t(23) > 3.27$, both $p \leq .005$, between which error costs did not differ significantly, $t(23) = 1.68$. Right-hand error costs were, however, significantly higher in these test blocks than in test block L_{trans}, both $t(23) > 3.18$, both $p \leq .05$, in which right-hand error costs were not significant, $t(23) < 1$. Significant left-hand error costs were present in test blocks LR_{rand} and L_{trans}, both $t(23) > 3.43$, both $p \leq .01$, between which error costs did not differ significantly, $t(23) = 0.42$. Left-hand error costs were, however, significantly higher in these test blocks than in test block R_{trans}, both $t(23) > 2.61$, both $p \leq .05$, in which left-hand error costs were not significant, $|t(23)| < 1$. Consistent with RT results, the transferred sequence did not have as detrimental an effect on performance as a pseudo-random sequence. Instead, performance suffered only for that hand with which a random sequence was executed while no performance decrements were evident for the other hand with which the transferred sequence was executed.

Completeness of Intermanual Transfer. An additional ANOVA on session 3 RT costs with repeated measures on the factors Sequence (fixed sequence practiced with the left hand vs. fixed sequence practiced with the right hand) and Hand Practice (fixed sequence executed with the practiced hand vs. with the unpracticed hand while the other hand executes a pseudo-random sequence) revealed no significant main effects or interactions, all $F < 1$. In particular, RT costs in transfer blocks L_{trans} and R_{trans} were not significantly higher than RT costs in test blocks R_{rand} and L_{rand}, respectively, as reflected in the non-significant main effect Hand Practice, $F(2, 46) = 0.35$, $\eta_p^2 = .015$, which suggests perfect intermanual transfer of independently acquired knowledge about the two hand-related sequences. There were no indications of a speed-accuracy trade-off which might have accounted for this pattern of RT costs: An ANOVA on session 3 error costs with repeated measures on the factors Sequence, Hand Practice, and Hand (left, right) revealed a significant three-way interaction, $F(1, 23) = 36.44$, $p \leq .001$, $\eta_p^2 = .613$, reflecting hand-specific error costs as already discussed in the results sections on independent sequence learning and intermanual transfer. The main effect Hand Practice and the interaction between the factors Hand and Sequence approached, but did not reach statistical significance, $F(1, 23) = 3.91$, $p \leq .060$, $\eta_p^2 = .145$, and, $F(1, 23) = 4.13$, $p \leq .054$, $\eta_p^2 = .152$, respectively. No other main effects or interactions were significant, all $F < 1.54$, all $\eta_p^2 < .063$.

Free Recall. Participants' performance in the post-experimental recall task was scored by determining the number of recalled triples which were part of the respective hand-related sequence. Six participants recalled the complete 6-element sequence, four participants recalled the complete 5-element sequence, and only two participants recalled both sequences completely. These twelve participants were considered as having explicit sequence knowledge. The remaining twelve participants recalled a mean number of 2.25 triples (out of 6; *SD* = 0.75) from the 6-element sequence and a mean number of 1.42 triples (out of 5; *SD* = 1.31) from the 5-element sequence. These participants were considered as having only fragmentary explicit sequence knowledge.

The Role of Explicit Sequence Knowledge. In order to assess whether the obtained results depended on the acquisition of explicit sequence knowledge, all analyses were repeated for the sub-sample of twelve participants who displayed only fragmentary explicit sequence knowledge. The same pattern of results was obtained as for the entire sample (see Figure 3B).

3.1.3 Discussion

In a bimanual version of the SRT task, participants executed two uncorrelated sequences of stimuli and responses simultaneously, one with the left hand and the other with the right hand. After extensive practice, either one of the two sequences or both were replaced with a pseudo-random sequence. The resulting RT costs were significantly larger when both sequences were randomized than when only one of the sequences was randomized. As participants suffered similarly from losing either of the two sequences and individual RT costs were not negatively correlated the data suggest independent learning of the two sequences. This conclusion is further supported by hand-related error costs, that is, left hand errors increased only when the sequence of the left hand was abolished and right hand errors increased only when the right-hand sequence was abolished.

Additionally, RT costs in transfer blocks in which the sequence practiced with the one hand was transferred (parallel-shifted, not mirrored) to the other hand (while the hand with which the transferred sequence had been practiced executed a pseudo-random sequence) were significantly smaller than when both sequences were abolished. This suggests that the acquired sequence knowledge allows for transfer between hands. Intermanual transfer was additionally confirmed by the fact that there were no significant error costs for that hand which executed a transferred sequence. In fact, the independently acquired knowledge about the two hand-related sequences appeared to be fully transferable between the hands.

Thus, the results of Experiment 1 are consistent with independent learning of two uncorrelated, hand-related sequences of stimuli and responses. As the same pattern of results was obtained for a sub-sample of participants who acquired only fragmentary explicit sequence knowledge, the underlying learning mechanisms presumably do not require the sequence structures to be recognized. Furthermore, the acquired sequence knowledge appeared to be effector-independent inasmuch as it was available for intermanual transfer. The question remains, then, what the acquired sequence knowledge may be based on. At least two possibilities are to be considered.

First, and probably most obvious, participants may have benefited from facilitation of the forthcoming stimulus locations for each of the two hands. Second, participants may have benefited from facilitation of the forthcoming responses for each hand, either by facilitation of the locations of the to-be-pressed keys (Willingham et al., 2000) or by facilitation of the to-be-moved fingers (R-R learning).

Experiment 2 was designed in order to disentangle the respective impact of stimulus and response facilitation on the observed sequence learning. For this purpose a new condition was introduced in which the responses of both hands were specified by only one stimulus so that there were no longer two different stimulus sequences available for separate learning. Secondly, longer and more complex sequences were used in Experiment 2 in order to make integrated learning of the compound sequence more unlikely. This should also render the acquisition of explicit sequence knowledge more difficult. Finally, the training was prolonged in order to increase the chances of obtaining a manifestation of non-transferable, hand-specific sequence knowledge.

3.2 Experiment 2

In Experiment 2 participants performed a bimanual SRT task essentially similar to the one described for Experiment 1 except for an additional variation of stimulus presentation: The dual-stimulus condition was a replication of Experiment 1, with two stimuli, one for each hand, appearing simultaneously on every trial. In contrast, in the single-stimulus condition the responses for the left and the right hand were specified by only one imperative stimulus. In both conditions participants practiced the same uncorrelated sequences, one with fingers of the left hand, the other with fingers of the right hand.

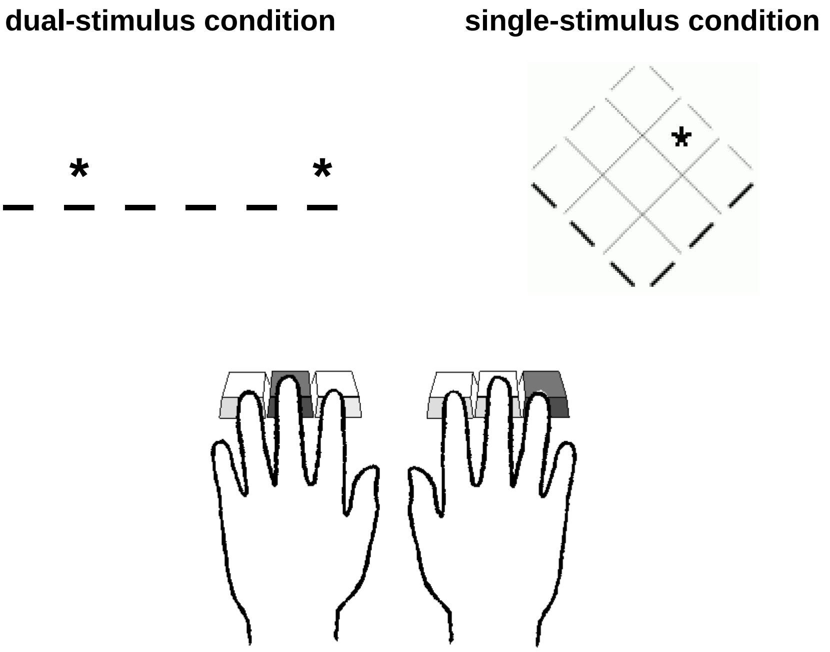
In the dual-stimulus condition, independent learning of the two sequences should occur, resulting in transferable sequence knowledge just like in Experiment 1. In the single-stimulus condition, however, which hardly allows for hand-related stimulus-stimulus (S-S) or response-stimulus (R-S) learning, weaker indications of (a) independent sequence learning and (b) intermanual transfer are to be expected, if and only if stimulus facilitation plays the crucial role for independent sequence learning.

3.2.1 *Method*

Because Experiment 2 was identical to Experiment 1 in most respects only the differences are described here.

Participants. Twenty-four individuals (mean age 23 years) volunteered to participate in Experiment 2 either in partial fulfillment of course requirements or for a payment of €25. Twenty participants reported to be predominantly right-handed, three asserted to be ambidextrous, and one participant was predominantly left-handed.

Apparatus and Materials. In the dual-stimulus condition, a pair of imperative stimuli (asterisks) appeared in two of six horizontally aligned locations. Unlike in Experiment 1, the six locations were not arranged in two groups of three. Instead, there was a distance of 6 mm between any two adjacent locations. Consequently, the visual separation of the two stimulus sequences was less obvious. In the single-stimulus condition, the imperative stimuli (asterisks) could appear in any one of nine cells in a 3x3 matrix displayed centered on the screen, standing on one of its vertices (see Figure 4). The length of each side of the cells was 15 mm. The rows and columns of the matrix were marked by straight lines 9 mm in length appearing at the lower left side and lower right side of the matrix, respectively.



dual-stimulus condition **single-stimulus condition**

Figure 4. Stimulus-response assignment in the two presentation modes in Experiment 2. The keys which participants were instructed to press simultaneously in response to the depicted stimulus display are colored dark gray.

The left-hand keys S, D, and F were assigned compatibly from left to right to the rows of the matrix (numbered 1, 2, 3, from left to right), while the right-hand keys J, K, and L were assigned compatibly from left to right to the columns of the matrix (also numbered 1, 2, 3, from left to right). In this way, a single stimulus specified both a response for the left hand and a response for the right hand.

In both conditions the sequences of the left and the right hand were determined by fixed sequences in regular blocks. An 8-element sequence (32131312) and a 9-element sequence (212132313) were used. In both sequences, prediction of the respective next element required the knowledge of up to four preceding elements so that the sequences were not only more complex but also better balanced than in Experiment 1. When presented simultaneously, these two uncorrelated sequences establish a compound sequence which repeats every 72 trials. Analyzing this compound sequence in terms of transition probabilities reveals that each of the 9 possible compound stimuli has 4 possible successors. Also, among the 28 occurring combinations of two consecutive compound stimuli (2-tuples) there are 13 with unique successors and 15 with at least two potential successors. Furthermore, among the 56 occurring 3-tuples there are still 14 with unique successors and 42 with at least two potential successors. Only at the level of 4-tuples is the compound sequence fully predictable as there is only one possible successor for each 4-tuple. So the compound sequence is a hybrid sequence containing unique first-order, second-order, and third-order conditional transitions.

The pseudo-random sequences were 144 elements long so that each matched the length of an entire test block. They were constructed to conform to properties of the fixed sequences they replaced as described for Experiment 1. Again, pseudo-random sequences were selected that shared as few quadruples (4-tuples) as possible with the to-be-replaced fixed sequence. Specifically, out of the total of 141 quadruples contained in each of the pseudo-random sequences selected to replace the 8-element sequence either 46 or 48 quadruples matched one of the 8 quadruples contained in the 8-element sequence. Similarly, each of the pseudo-random sequences replacing the 9-element sequence contained either 29 or 31 quadruples (out of a total of 141) matching one of the 9 quadruples in the 9-element sequence. The same pseudo-random sequences were used for each participant.

Procedure. Half of the participants were assigned to the dual-stimulus and the single-stimulus condition each. Within each condition, half of the participants practiced the 8-element sequence with the left hand and the 9-element sequence with the right hand while the assignment was reversed for the other participants.

Session 1 started with a warm-up block in which pseudo-random sequences were presented for both hands, followed by 15 fixed-sequence blocks. Session 2 comprised 20 fixed-sequence blocks. Session 3 started with five fixed-sequence blocks, and beginning with the sixth block (i.e., after 720 repetitions of the 8-element sequence and 640 repetitions of the 9-element sequence), five test blocks alternated with five fixed-sequence blocks. These test blocks were: L_{rand}, R_{rand}, LR_{rand}, L_{trans}, and R_{trans}. The order of the first three and the last two of these test blocks was counterbalanced across participants independently of each other.

Each fixed-sequence block comprised 144 trials, as did all of the test blocks. The warm-up block contained only 72 trials. Each fixed-sequence block began at a randomly determined position in the 72-element compound sequence established by the two hand-related sequences.

Prior to session 1, participants received written instructions presented on the screen. For the dual-stimulus condition these were exactly the same as in Experiment 1. Participants in the single-stimulus condition were additionally informed about the assignment of rows and columns in the matrix to keys on the keyboard and to fingers of the two hands as described above. After completing the SRT task in session 3, participants completed a sequence recall task as described for Experiment 1.

3.2.2 Results

RT and error data were prepared as described for Experiment 1. In the dual-stimulus condition RTs from 7.7% of trials were excluded (4.4% error trials, 1.8% outlier RTs, 1.5% trials with asynchronous responses) and in the single-stimulus condition RTs from 9.1% of trials were excluded (5.9% error, 2.0% outlier, 1.2% asynchronous). The means of the individual median RTs in each block are shown in Figure 5. As described for Experiment 1, RT costs for each test block were computed as the difference between the median RT in that test block and the mean of the median RTs in the baseline regular blocks. For test blocks L_{rand}, R_{rand}, and LR_{rand}, all adjacent blocks provided the data for the baseline (i.e., blocks 41, 43, 45, and 47). Accordingly, for the test blocks L_{trans} and R_{trans}, the adjacent blocks 47, 49, and 51 constituted the baseline. Error costs were computed in a manner analogous to RT costs. Again, none of the error cost variables differed significantly from a normal distribution, all Kolmogorov-Smirnov Zs between 0.481 and 1.152, all $p > .140$. Therefore, parametric analyses were computed with the degrees of freedom in repeated-measures ANOVAs adjusted for violations of the sphericity assumption as for Experiment 1. Also, p-values were subjected to the Bonferroni adjustment for each family of pairwise comparisons (paired-samples t-tests).

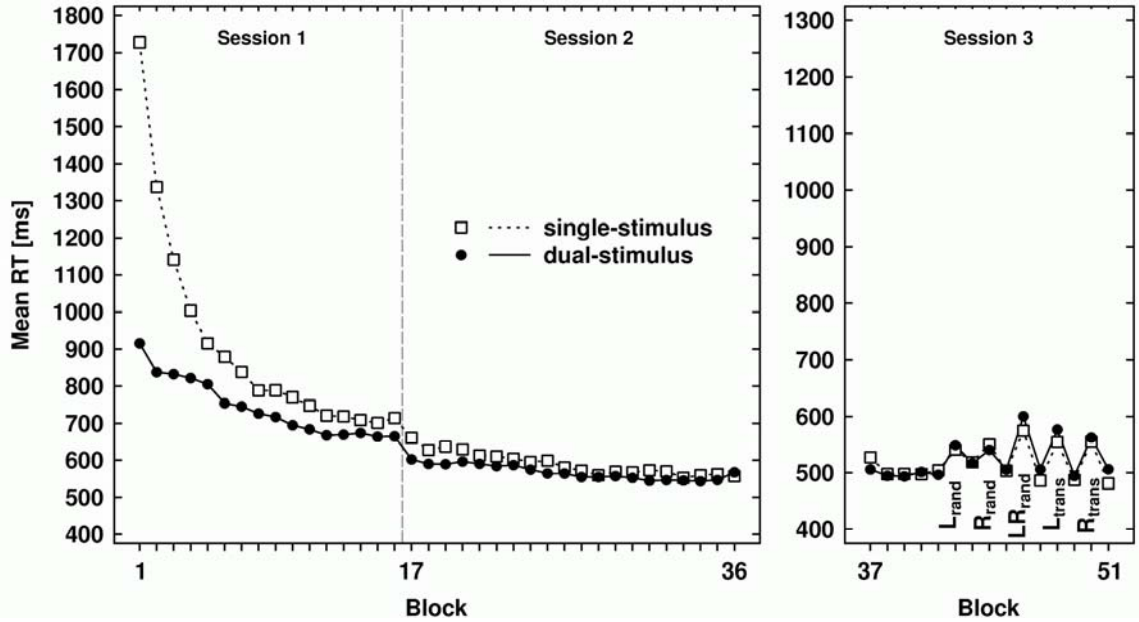


Figure 5. Means of individual median RTs in Experiment 2 separately for the two presentation modes. For presentation purposes, test blocks are ordered in a consistent manner; in reality, the order of test blocks was counterbalanced across participants. The ordinate's scale has been adjusted for data from session 3 (blocks 37–51) to aid comparison with data from Experiment 1.

There were significant RT costs in every test block when including data from both presentation modes (the dual-stimulus and the single-stimulus condition), all $t(23) > 6.38$, all $p \leq .001$, as well as when analyzing RT costs separately for each presentation mode, all $t(11) > 3.75$, all $p \leq .01$. For relevant RT cost means and error cost means see Figure 6 and Figure 7A.

Randomization Probes: RT Costs. A mixed-factors ANOVA on RT costs with repeated measures on the factor Test Block (L_{rand}, R_{rand}, LR_{rand}) and with Presentation Mode (dual-stimulus condition, single-stimulus condition) as the between-subjects factor revealed a significant main effect Test Block, $F(2, 44) = 25.88$, $p \leq .001$, $\eta_p^2 = .541$, indicating higher RT costs in test block LR_{rand} than in test block L_{rand} and R_{rand}, both $t(23) > 5.56$, both $p \leq .001$, between which RT costs did not differ significantly, $t(23) = 0.24$. The main effect Presentation Mode was not significant, $F(1, 22) = 0.29$, $\eta_p^2 = .013$, but the interaction was, $F(2, 44) = 3.27$, $p \leq .05$, $\eta_p^2 = .129$.

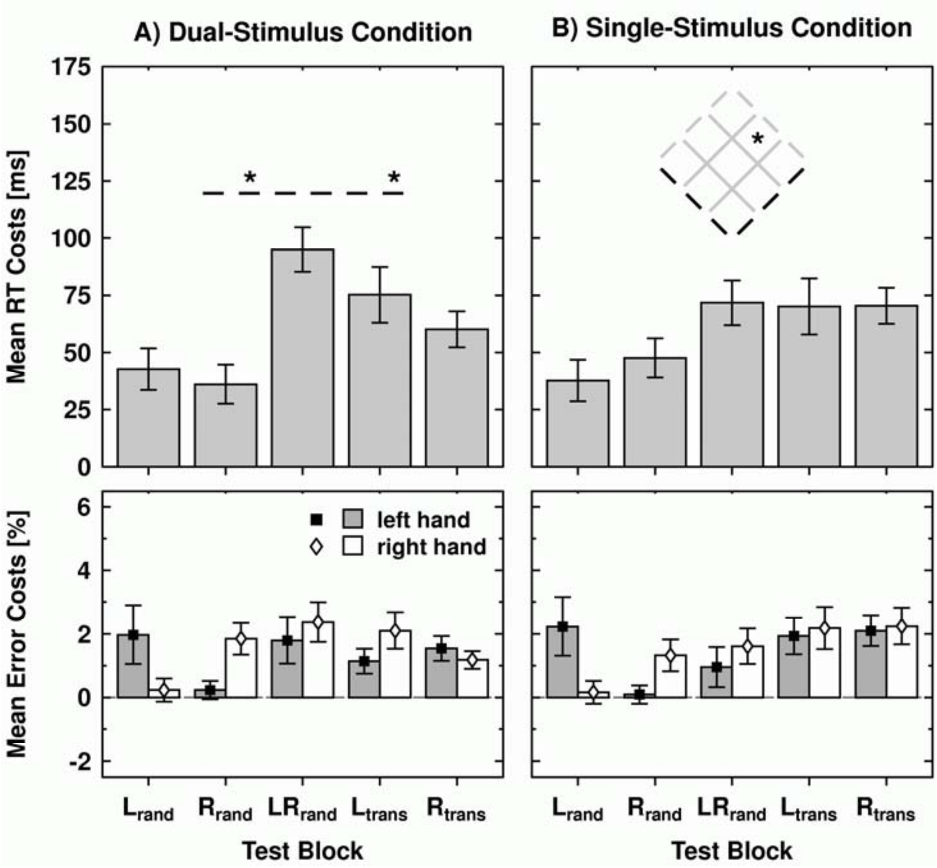


Figure 6. Mean RT and error costs in each of the test blocks in Experiment 2 separately for the dual-stimulus (A) and the single-stimulus (B) presentation mode. Error bars represent standard errors of the means.

In order to unpack this interaction, separate ANOVAs on RT costs with repeated measures on the factor Test Block were computed for both presentation modes. In the dual-stimulus condition the data pattern of Experiment 1 was repeated: the main effect Test Block was significant, $F(2, 22) = 25.84$, $p \leq .001$, $\eta_p^2 = .701$, indicating that RT costs did not differ significantly between blocks L_{rand} and R_{rand}, $t(11) = 0.77$, but were lower in these blocks than in block LR_{rand}, both $t(11) > 5.99$, both $p \leq .001$. In the single-stimulus condition the main effect Test Block was also significant, $F(2, 22) = 5.88$, $p \leq .01$, $\eta_p^2 = .349$, and RT costs did not differ between blocks L_{rand} and R_{rand}, $t(11) = 0.93$. However, in contrast to the dual-stimulus condition, only in block L_{rand} were RT costs lower than in block LR_{rand}, $t(11) = 3.21$, $p \leq .05$, whereas the difference between blocks R_{rand} and LR_{rand} missed significance, $t(11) = 2.60$, $p \leq .074$. Furthermore, the mean difference between RT costs in blocks L_{rand} and R_{rand} on the one hand and block LR_{rand} on the other hand was substantially smaller in the single-stimulus condition ($M = 29.1$ ms) than in the dual-stimulus condition ($M = 55.5$ ms), $F(1, 22)$

= 5.14, $p \leq .05$, $\eta_p^2 = .189$, although RT costs in LR_{rand} blocks did not differ significantly between the two conditions, $t(22) = 1.68$, $p \leq .107$.

There was no negative correlation between individual RT costs in test blocks L_{rand} and R_{rand}, $r(24) = .374$, $p \leq .072$ (dual-stimulus condition: $r(12) = .477$, $p \leq .117$; single-stimulus condition: $r(12) = .341$, $p \leq .278$), indicating that there was no trade-off between learning of the left-hand sequence and learning of the right-hand sequence.

Randomization Probes: Error Costs. A mixed-factors ANOVA on error costs with repeated measures on the factors Hand (left, right) and Test Block and with Presentation Mode as the between-subjects factor revealed a significant interaction between the factors Hand and Test Block, $F(2, 44) = 8.38$, $p \leq .005$, $\eta_p^2 = .276$, $\varepsilon_{GG} = .767$. The main effect Test Block approached but did not reach significance, $F(2, 44) = 2.66$, $p \leq .081$, $\eta_p^2 = .108$. No other main effects or interactions were significant, all $F < 0.80$, all $\eta_p^2 < .035$.

In order to further analyze the significant interaction, separate ANOVAs with repeated measures on the factor Test Block were computed for left-hand and for right-hand error costs. Because there were no significant interactions involving Presentation Mode this factor was dropped from subsequent analyses. Therefore, relevant means are those computed across the two presentation modes and depicted in Figure 7A.

The ANOVA for left-hand error costs revealed a significant main effect Test Block, $F(2, 46) = 4.97$, $p \leq .05$, $\eta_p^2 = .178$, indicating significant costs in test blocks L_{rand} and LR_{rand}, both $t(23) > 2.85$, both $p \leq .01$, but not in block R_{rand}, $t(23) = 0.79$, $p \leq .437$. Costs in block L_{rand} but not in block LR_{rand} were significantly higher than in block R_{rand}, $t(23) = 2.89$, $p \leq .05$, and t(23) = 2.26, p ≤ .10, respectively. Costs did not differ between blocks L_{rand} and LR_{rand}, $t(23) = 1.12$.

The ANOVA for right-hand error costs revealed a significant main effect Test Block, $F(2, 46) = 8.42$, $p \leq .001$, $\eta_p^2 = .268$, indicating significant error costs in test blocks R_{rand} and LR_{rand}, both $t(23) > 4.56$, both $p \leq .001$, which did not differ from each other, $t(23) = 1.09$, but which were significantly higher than those in test block L_{rand}, both $t(23) > 2.83$, both $p \leq .05$, for which there were no significant error costs, $t(23) = 0.78$, $p \leq .445$. Thus, as in Experiment 1, performance suffered only for that hand which lost its sequence while performance with the other hand, which retained its sequence, was unaffected.

Transfer Probes: RT Costs. A mixed factors ANOVA on RT costs with repeated measures on the factor Transfer Block (LR_{rand}, L_{trans}, R_{trans}) and with Presentation Mode (dual-stimulus condition, single-stimulus condition) as the between-subjects factor revealed a significant main effect Transfer Block, $F(2, 44) = 4.91$, $p \leq .05$, $\eta_p^2 = .182$. The critical Transfer Block × Presentation Mode interaction was significant, $F(2, 44) = 4.18$, $p \leq .05$, $\eta_p^2 = .160$. The main effect Presentation Mode was not significant, $F(1, 22) = 0.22$, $\eta_p^2 = .010$.

In order to unpack the significant Transfer Block × Presentation Mode interaction, separate ANOVAs on RT costs with repeated measures on the factors Block Half (first, second) and Transfer Block were computed for data from each presentation mode. The factor Block Half was included to evaluate the within-block learning account of intermanual transfer as discussed for Experiment 1.

For data from the dual-stimulus condition, the ANOVA revealed a significant main effect Transfer Block, $F(2, 22) = 11.24$, $p \leq .001$, $\eta_p^2 = .505$, indicating that RT costs were significantly higher in test block LR_{rand} than in test blocks L_{trans} and R_{trans}, both $t(11) > 3.07$, both $p \leq .05$. RT costs did not differ significantly between test blocks L_{trans} and R_{trans}, $t(11) = 1.47$. That is, as in Experiment 1, performance suffered less when executing the transferred sequence together with a pseudo-random sequence than when executing two pseudo-random sequences, thus indicating intermanual transfer. In contrast, for data from the single-stimulus condition there was no evidence for intermanual transfer as the main effect Transfer Block was not significant, $F(2, 22) = 0.01$, $\eta_p^2 = .001$.

In the dual-stimulus as well as in the single-stimulus condition neither the main effect Block Half was significant, both $F(1, 11) < 0.24$, both $\eta_p^2 < .022$, nor was the Block Half × Transfer Block interaction significant, $F(2, 22) = 2.63$, $p \leq .095$, $\eta_p^2 = .193$, and $F(2, 22) = 3.37$, $p \leq .053$, $\eta_p^2 = .235$, respectively. Thus, there were no reliable indications of within-block learning in transfer blocks.

Transfer Probes: Error Costs. A mixed factors ANOVA on error costs with repeated measures on the factors Hand (left, right), Block Half (first, second), and Transfer Block, and with Presentation Mode as the between-subjects factor was computed. The interaction between the factors Transfer Block and Presentation Mode approached but did not reach significance, $F(2, 44) = 3.01$, $p \leq .06$, $\eta_p^2 = .120$. The other main effects and interactions were not significant either, all $F < 2.78$, all $\eta_p^2 < .113$. Separate ANOVAs with repeated measures on the factors Hand and Test Block for the dual-stimulus and the single-stimulus condition revealed no significant effects, all $F < 3.18$, all $\eta_p^2 < .225$.

Completeness of Intermanual Transfer. An additional mixed factors ANOVA on RT costs with repeated measures on the factors Sequence (fixed sequence practiced with the left hand vs. fixed sequence practiced with the right hand), and Hand Practice (fixed sequence executed with the practiced hand vs. with the unpracticed hand while the other hand executes a pseudo-random sequence), and with Presentation Mode (dual-stimulus condition, single-stimulus condition) as the between-subjects factor revealed a significant main effect Hand Practice, $F(1, 22) = 23.70$, $p \leq .001$, $\eta_p^2 = .519$, reflecting that RT costs were smaller when a fixed sequence is executed with the hand with which it had been practiced (R_{rand} and L_{rand}; $M = 41.1$ ms) than when executed with the respective other hand (L_{trans} and R_{trans}, respectively; $M = 68.9$ ms). The interaction between the factors Sequence, Hand Practice, and Presentation Mode approached but did not reach statistical significance, $F(1, 22) = 4.05$, $p \leq .057$, $\eta_p^2 = .155$. No other main effects or interactions were significant, all $F < 0.61$, all $\eta_p^2 < .027$. There were no indications of a speed-accuracy trade-off which might have accounted for this pattern of RT costs.

Free Recall. None of the participants recalled either of the two sequences completely. In order to split the sample into two sub-samples as in Experiment 1, participants were considered as possessing noticeable explicit sequence knowledge if they recalled 3 or more quadruples from the 8-element or 4 or more quadruples from the 9-element sequence. The other participants were considered as possessing little explicit sequence knowledge.

In the dual-stimulus condition, six participants possessed noticeable explicit sequence knowledge. They recalled a mean number of 2.7 quadruples (out of 8; $SD = 1.21$) from the 8-element sequence and a mean number 4.8 quadruples (out of 9; $SD = 0.75$) from the 9-element sequence. The remaining six participants with little explicit sequence knowledge recalled a mean number of 1.2 quadruples (out of 8; $SD = 0.41$) from the 8-element sequence and a mean number of 1.5 quadruples (out of 9; $SD = 1.05$) from the 9-element sequence.

In the single-stimulus condition seven participants were classified as possessing noticeable explicit sequence knowledge: They recalled a mean number of 3 quadruples (out of 8; $SD = 1.29$) from the 8-element sequence and a mean number 5 quadruples (out of 9; $SD = 1.15$) from the 9-element sequence. The remaining five participants recalled a mean number of 1.8 quadruples (out of 8; $SD = 0.45$) from the 8-element sequence and a mean number of 1.8 quadruples (out of 9; $SD = 1.30$) from the 9-element sequence.

The Role of Explicit Sequence Knowledge. The sub-sample of participants with only little explicit sequence knowledge showed almost the same data pattern as the entire sample (see Figure 7B).

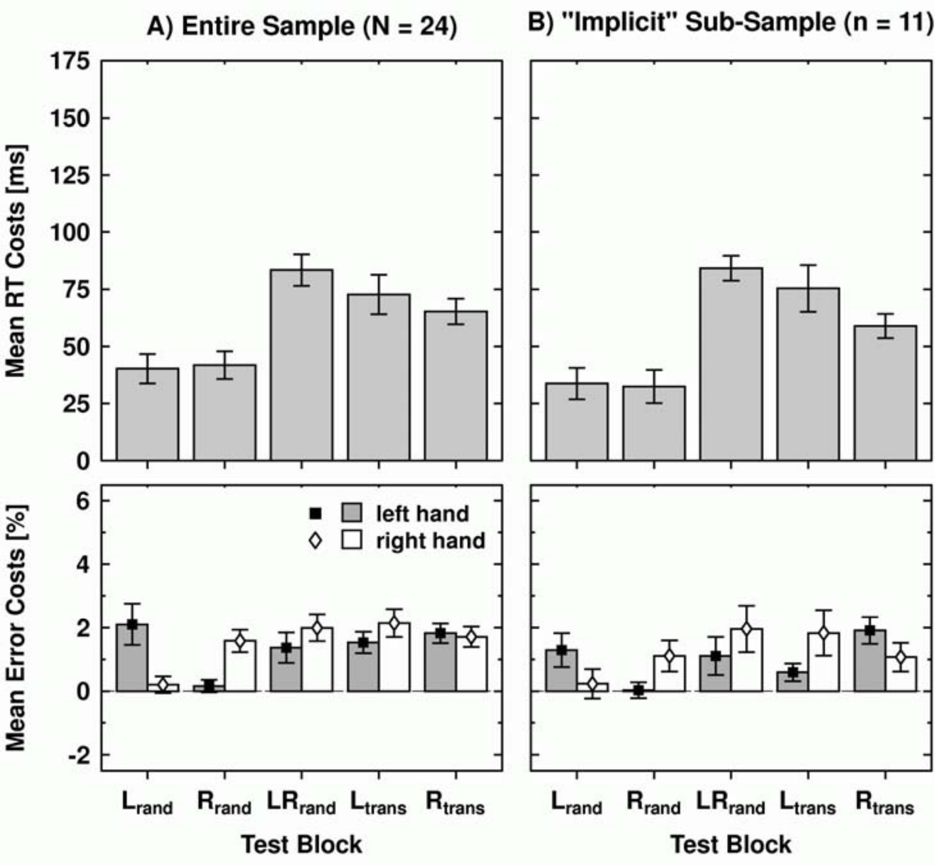


Figure 7. Mean RT and error costs in each of the test blocks in Experiment 2 separately for the entire sample (A) and for the sub-samples of participants who possessed only little explicit knowledge about the sequences (B). Error bars represent standard errors of the means.

3.2.3 Discussion

Participants performed a bimanual-bisequential SRT task with either two distinct stimuli or only one stimulus specifying the required simultaneous responses of the left and the right hand. Following extensive practice, independent learning of the two sequences was tested in a series of test blocks. RT costs were higher when both sequences were replaced with a pseudo-random sequence than when only one of the sequences was abolished, thus indicating independent learning of the two sequences. As in Experiment 1, a trade-off between learning of the left-hand and the right-hand sequence can be ruled out as individual RT costs in the test blocks with only one of the sequences abolished were not negatively correlated. The same pattern of results was obtained for a sub-sample with only little if any explicit sequence knowledge. Therefore, learning of the hand-related sequences is presumably independent of the recognition of the sequences.

Concerning the two stimulus presentation modes, the critical increase of RT costs with both compared to only one of the sequences randomized turned out to be clearly more pronounced with two stimuli compared to one stimulus, although the pattern of hand-related error costs corroborates the conclusion that independent sequence learning had occurred in both conditions.

Intermanual transfer was also significantly influenced by the stimulus presentation mode: Transfer from the practiced to the unpracticed hand was evident in the dual-stimulus condition whereas in the single-stimulus condition, the data provided no evidence for intermanual transfer. This finding is in line with the notion that the hand-related but nevertheless transferable sequence knowledge found in Experiment 1 and in the dual-stimulus condition of Experiment 2 most probably relies on the facilitation of forthcoming stimuli in the hand-related stimulus sequences. This can take the form of both S-S and R-S learning. If there is only one stimulus for both sequences, separate hand-related stimulus sequences no longer exist so that neither hand-related S-S nor R-S learning can take place. Nevertheless, the data, in particular the error costs, suggest that also in the single-stimulus condition hand-related sequence knowledge has been acquired. As such knowledge could hardly rely on stimulus facilitation (i.e., S-S or R-S learning) it most likely reflects response facilitation (R-R learning), that is, hand-specific motor sequence knowledge which does not lend itself to intermanual transfer.

It deserves mention that intermanual transfer was weaker in the dual-stimulus condition of Experiment 2 than in Experiment 1. This becomes especially apparent if RT costs in transfer blocks L_{trans} and R_{trans} are compared with RT costs in test blocks R_{rand} and L_{rand}, respectively, that is, if one compares performance decrements resulting from executing with one hand a regular and with the other hand a random sequence depending on whether the regular sequence is performed by the hand which has previously practiced this sequence or by the other hand which has previously practiced the other sequence. In Experiment 1 there was no significant difference between these two conditions (see Figure 3), suggesting that intermanual transfer was complete. In contrast, in Experiment 2 (see Figure 7A), transfer blocks L_{trans} and R_{trans} yielded higher RT costs than test blocks R_{rand} and L_{rand}.

This incompleteness of intermanual transfer can be accounted for by the same reasoning as the failure of transfer in the single-stimulus condition, that is, it can be argued that despite the presentation of separate stimuli, learning of transferable hand-related stimulus sequences has been hampered compared to Experiment 1 for the following reasons: first, because the separation of the hand-related stimuli was less obvious; second, because the amount of training was increased which is known to make the occurrence of effector-specific (non-transferable) sequence knowledge more likely (e.g., Bapi et al., 2000; Park & Shea, 2005); and third, because the amount of explicit sequence knowledge was substantially reduced, which has also been suggested to make implicit effector-specific learning more prominent (cf. Hikosaka et al., 2002).

One must consider the possibility that the performance decrements in transfer blocks might not be due to a failure of transfer but rather to interference: first, for the transfer hand the formerly practiced sequence might interfere with the new transferred sequence; second, the transferred sequence might become suppressed because the hand which has practiced this sequence before, now has to perform a random sequence. However, the interference account can hardly explain why in transfer blocks of Experiment 1 no interference at all is indicated. In particular, in Experiment 1 the error data suggested complete transfer as there were no significant error costs for that hand which performed the transferred sequence, whereas error costs were significant for the hand which performed the random sequence. Therefore, I consider the account in terms of incomplete transfer at least as plausible as the interference account.

Some aspects of the reported data pattern might also have been due to learning of the compound bimanual sequence instead of separate learning of two hand-related sequences. Although it is not possible to rule out that at least parts of the compound sequence may have been learned, compound learning does not provide a satisfactory account for all findings. First, it stands to reason that compound learning in Experiment 2 should have been easier and thus more pronounced in the single-stimulus condition than in the dual-stimulus condition, which was clearly not the case. Numerically, the difference was even in the opposite direction. Second, the transitions of the compound sequence were changed in equal measure both in transfer blocks (L_{trans} and R_{trans}) and in test block LR_{rand}, so that the same costs should result. However, Experiment 1 and the dual-stimulus condition of Experiment 2 showed substantially greater RT costs in block LR_{rand} than in transfer blocks. One may argue that the reduced costs in the transfer blocks are due to within-block learning. However, there were no reliable indications of within-block learning. Furthermore, within-block learning of a compound sequence should have reduced error costs for both hands whereas error costs were selectively reduced for that hand only which performed the transferred sequence. In sum, the data pattern reported here appears to be more consistent with the independent sequence learning than with the compound learning account.

In conclusion, Experiment 2 yielded a data pattern consistent with the notion of hand-related sequence knowledge which could be transferred to the other hand only partly (dual-stimulus condition) or not at all (single-stimulus condition). The amount of transferable sequence knowledge was reduced in favor of non-transferable sequence knowledge when the two response sequences were triggered by a single stimulus instead of two stimuli, so that the acquisition of hand-related stimulus codes is impeded. In terms of Keele et al.’s (2003) model: When there is only a single stimulus there is virtually no basis for the establishment of separate stimulus-based learning modules. As the order in which the keys assigned to the respective hand are to be pressed (cf. Willingham et al., 2000) should be as effectively transferable as the order of stimulus locations and intermanual transfer should not have been complete in Experiment 1 if sequence knowledge in terms of response locations (i.e., keys to be pressed) was not available for intermanual transfer, it appears more likely that the non-transferable sequence knowledge relies on the order in which the fingers of the respective hand have to act. Consequently, any independent learning of the two sequences would have to be ascribed to the operation of separate learning modules for the left and the right hand. The interpretation that after extensive practice participants may have acquired sequence knowledge which is specific to the hand with which it has been acquired fits well with the speculation of Keele et al. (2003, p. 317) that “distinctions within the motor system (e.g., hands vs. feet) may also constitute dimensions”.

4 Experiments 3–5: Alternating Bimanual-Bisequential SRT Task

The findings from Experiments 1 and 2 provided initial evidence consistent with the existence and operation of separate learning modules for the left and the right hand. Non-transferable, effector-specific sequence knowledge developed under conditions of extensive practice and low perceptual separability of the two hand-related sequences. The next set of experiments was designed to subject these observations to further testing. In particular, the experiments were aimed at assessing the robustness of motor-based independent learning of hand-related sequences by creating increasingly unfavorable conditions for its occurrence. To this end, three manipulations were introduced: Independent learning of hand-related sequences was tested under conditions of alternating stimulus presentation and responding so that the stimuli/responses belonging to a hand-related sequence are separated by intervening stimuli/responses belonging to the other hand-related sequence, which might favor integrated over independent sequence learning. In Experiment 3, this alternating bimanual-bisequential

SRT task was implemented for hand-related sequences of different length which entails that the two sequences are largely uncorrelated. In Experiment 4, hand-related sequences of the same length were used so that the two sequences are highly correlated as is probably more representative of everyday multi-effector sequential actions and which might additionally favor the acquisition of integrated sequence learning. Finally, in Experiment 5, sequence stimuli appeared alternately with random stimuli; under these conditions, the supposed existence and operation of separate sequence learning modules for each hand should express itself in a benefit for learning the sequence when the assignment is such that responding to sequence stimuli involves only fingers of one hand compared to when the assignment is such that responding to sequence stimuli involves fingers of both hands.

4.1 Experiment 3

On each trial in Experiment 3, participants responded to a single imperative stimulus appearing in one of six locations on the monitor by pressing the corresponding key. Each of the three left-most keys was pressed with a different finger of the left hand, while each of the three remaining keys was pressed with a different finger of the right hand. As far as these aspects of the setting are concerned the task is isomorphic to a standard SRT task. An additional constraint was that the imperative stimulus appeared alternately on the left-hand side and on the right-hand side. Furthermore, unbeknownst to participants, the stimuli appearing on the left-hand side followed a fixed repeating sequence independently of the stimuli on the right-hand side, which followed a different uncorrelated sequence. This setup bears some resemblance to the single-stimulus condition in Experiment 2 inasmuch as only one imperative stimulus is present in each trial and therefore no separate S-S or R-S learning of the two hand-related sequences is possible. In contrast to Experiment 2, however, only one response is required on each trial, and participants respond alternately with the left and the right hand to different interleaved hand-related sequences.

If the two hand-related sequences are learned independently of one another, replacing one of them while retaining the other should incur costs (i.e., an increase in RT and error rate relative to when the sequence is present) only for that hand which loses its sequence, but not for the other hand. Furthermore, if any such independently acquired sequence knowledge is represented in an effector-independent (i.e., transferable) manner, transferring one hand-related sequence from the practiced hand to the other hand should not incur costs for that other hand. In contrast, integrated learning of the compound sequence spanning both hands would entail costs for both hands even if only one of the hand-related sequences was randomized. Also, to the extent that learning is integrated, there cannot be any intermanual transfer.

Integrated learning is not particularly likely, however, given the length and complexity of the compound sequence constituted by the uncorrelated hand-related sequences as discussed in detail below.

4.1.1 Method

Experiment 3 is largely a replication of Experiment 1 under conditions of alternating instead of simultaneous responding with the left and the right hand, and only the deviations from Experiment 1 will be described.

Participants. A total of 24 individuals (mean age 23.8 years) volunteered to participate in Experiment 1 in partial fulfillment of course requirements. Twenty-one participants reported to be predominantly right-handed, 1 professed to be ambidextrous, and the remaining 2 declared to be predominantly left-handed.

Task and Design. As already described, on each trial participants responded to a single imperative stimulus appearing in one of six locations on the monitor by pressing the corresponding key. Stimulus presentation was arranged such that participants responded alternately with the left and the right hand to different interleaved hand-related sequences. Again, the presence or absence of the hand-related sequences constituted the within-subjects factor. The same types of test blocks were implemented as in Experiments 1 and 2.

Apparatus and Materials. Stimulus presentation and response registration was controlled by the ERTS software package (Beringer, 1996). The six keys A, S, D, J, K, L on a standard QWERTZ keyboard served as response keys and were assigned from left to right to the six lines (locations) on the screen. There was an equal distance of 7 mm between any two adjacent lines on the screen. The keys were operated from left to right with the ring, middle, and index finger of the left hand and the index, middle, and ring finger of the right hand. The three left-hand locations will be referred to as L1, L2, and L3; the three right-hand locations will be referred to as R1, R2, and R3.

The same sequences were used as in Experiment 1 (32121 and 121323). Together the two hand-related sequences establish a compound sequence which spans both hands and repeats every 60 trials (e.g., L3 R1 L2 R2 L1 R1 L2 R3 L1 R2 L3 R3 L2 R1 L1 R2 L2 ...). The high level of complexity of this compound sequence can be characterized as follows: For each of the 12 possible combinations of two consecutive elements (2-tuples) there are two potential successor elements. When considering 3-tuples, there are 18 with two potential successors and only 6 with unique successors. Both among the 42 4-tuples and among the 54 5-tuples there are still six with two potential successors. Only at the level of 6-tuples is the compound sequence fully predictable as there is only one possible successor for each 6-tuple. So the compound sequence is a hybrid sequence containing unique third-order, fourth-order, fifth-order, and sixth-order conditional transitions.

When only one of the fixed, hand-related sequences was randomized, random trials for one hand alternated with sequence trials for the other hand. Each pseudo-random sequence was 60 elements long so that it matched the number of trials through which the to-be-replaced hand-related sequence would have cycled over the length of an entire 120-trial test block. Furthermore, pseudo-random sequences were constructed to resemble the sequences they replaced in that stimuli appeared with the same frequency and consecutive elements were never identical. From a large set of such pseudo-random sequences as many were selected as there were test blocks in the experiment under the constraint that the selected pseudo-random sequences shared as few triples as possible with the to-be-replaced hand-related sequence. Specifically, out of the total of 58 triples (3-tuples) contained in each of those pseudo-random sequences selected to replace the 5-element sequence, either 29 or 30 triples matched one of the 5 triples contained in the 5-element sequence. Similarly, each of those pseudo-random sequences replacing the 6-element sequence contained either 30 or 34 triples matching one of the 6 triples in the 6-element sequence.

Procedure. The experiment was conducted in two sessions scheduled for consecutive days. Session 1 started with a warm-up block in which pseudo-random sequences were presented for both hands, followed by 24 fixed-sequence blocks. Session 2 started with 16 fixed-sequence blocks. Beginning with the 17th block, three test blocks (L_{rand}, R_{rand}, LR_{rand}) alternated with three fixed-sequence blocks. The order of presentation of these test blocks was counterbalanced across participants. Finally, blocks 23 and 25 were test blocks of the L_{trans} and R_{trans} type, the order of which was counterbalanced across participants independently of the counterbalancing of the first four test blocks. The session concluded with a final fixed-sequence block.

Each fixed-sequence block comprised 120 trials (60 with the left hand and 60 with the right hand), so that participants completed 480 repetitions of the 5-element sequence and 400 repetitions of the 6-element sequence prior to the presentation of the first test block. All of the test blocks as well as the warm-up block also comprised 120 trials each. Each fixed-sequence block began at a randomly determined position in the compound 60-element sequence. Each trial began with the presentation of the imperative stimulus. Following the participant's response, 50 ms elapsed before the next trial was initiated. In case of an error, the German word for error ("Fehler!") appeared in red color centered below the row of location lines accompanied by a short beep tone for the duration of this response-stimulus interval.

In each session participants paused for at least 15 seconds between blocks. During that time a text on the screen informed participants about their mean RT as well as the number of errors in the previous block and reminded them of the requirements regarding speed and accuracy. After completing the SRT task, participants completed a sequence recall task as described for Experiment 1.

4.1.2 Results

RTs from error trials (3.6%) were excluded from analysis, as were RTs more than 3 *SD* above or below the *z*-transformed mean RT as determined separately for each participant, each block, and each hand (1.5%). For each family of pairwise comparions *p*-values were subjected to the Bonferroni adjustment. Unless otherwise noted all single-sample *t*-tests and all pairwise comparisons are one-tailed whenever directional hypotheses have been formulated. As in Experiments 1 and 2, the Greenhouse-Geisser correction was applied in repeated-measures analyses of variance (ANOVA) whenever necessary.

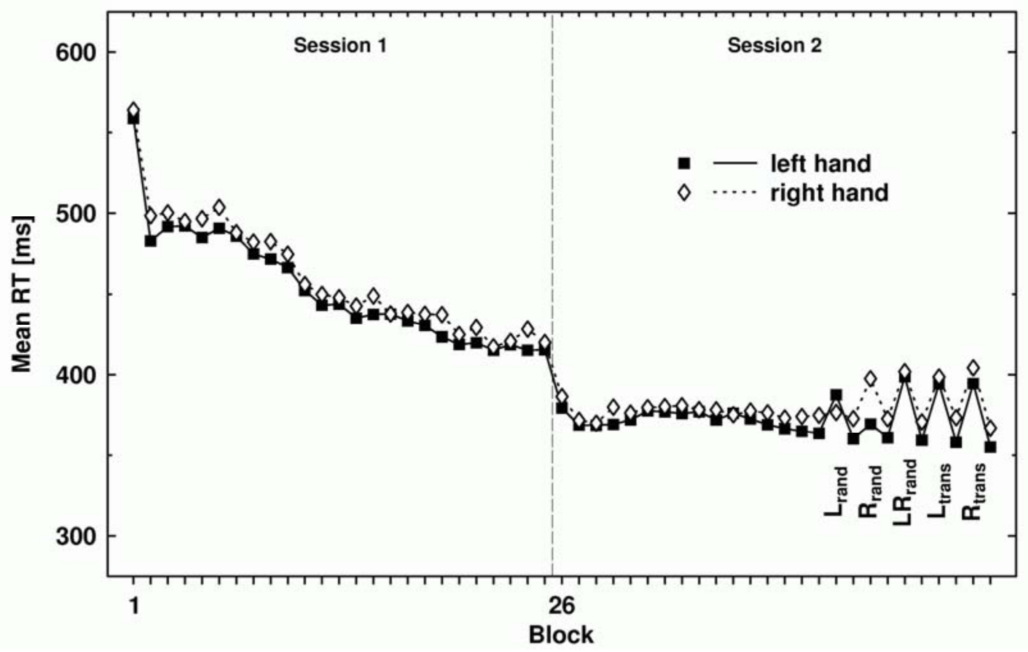


Figure 8. Means of individual median RTs in Experiment 3 separately for the left and the right hand. For presentation purposes, test blocks are ordered in a consistent manner; in reality, the order of test blocks was counterbalanced across participants.

Median RTs and error rates in each block were computed separately for left-hand and for right-hand responses. The means of the individual median RTs are shown in Figure 8 for each block across the experiment. RT costs as an index of sequence learning were computed as the difference between the median RT in a test block and the mean of the median RTs in the corresponding baseline blocks (session 2 blocks 16, 18, 20, and 22 for test blocks L_{rand}, R_{rand}, and LR_{rand}; session 2 blocks 22, 24, and 26 for test bocks L_{trans} and R_{trans}). Costs in terms of error rate were computed in an analogous manner. None of the error cost variables differed significantly from a normal distribution, all Kolmogorov–Smirnov *Z*s between 0.33 and 1.21, all $p > .109$. Therefore, error data were analyzed with parametric statistical tests. Relevant means are given in Figure 9.

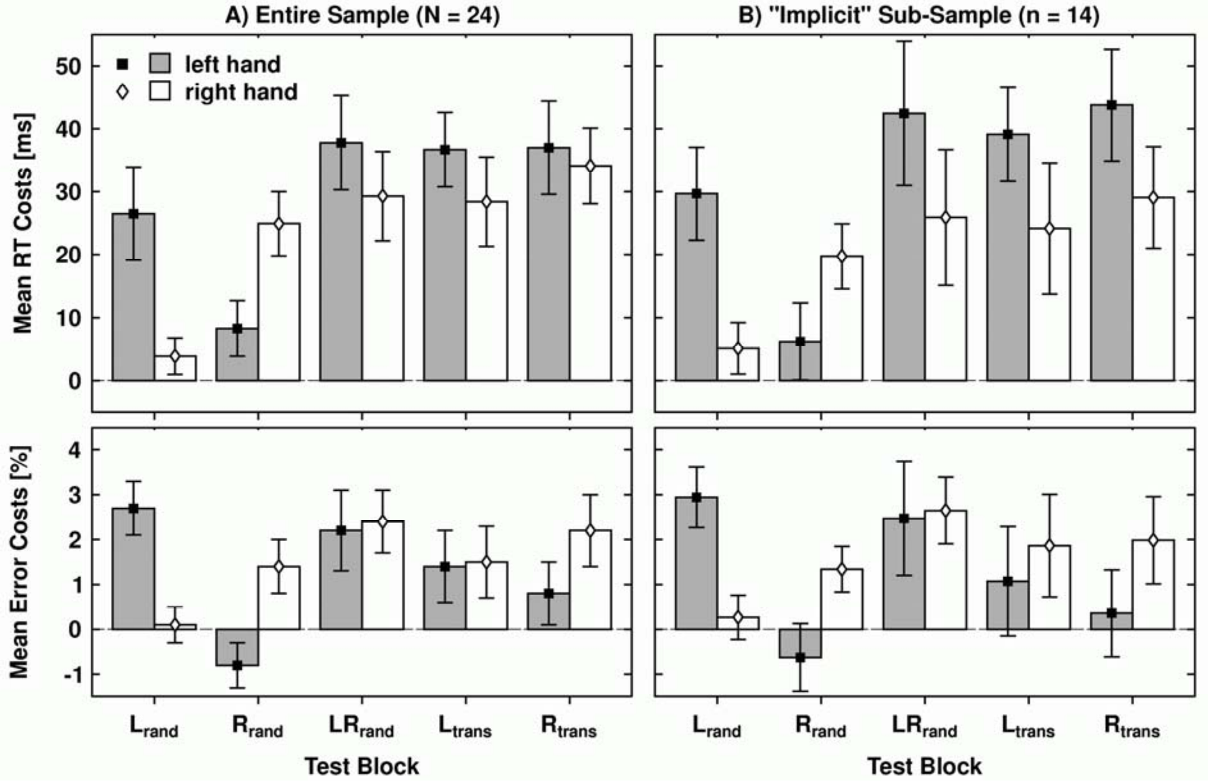


Figure 9. Mean RT and error costs in each of the test blocks in Experiment 3 separately for the left and the right hand; separately for the entire sample (A) and the sub-sample of participants who possessed little explicit knowledge about the sequences (B). Error bars represent standard errors of the means.

Essentially identical patterns of randomization costs were obtained both in RT data and in error data. Indications for a speed-accuracy trade-off emerged in test block R_{rand}. Therefore and for the sake of brevity, the analyses of RT and error data are presented together. Unlike Experiments 1 and 2, RT costs were not significant in all test blocks so single-sample *t*-tests will be presented first.

Randomization Probes: RT and Error Costs. There were significant left-hand RT and error costs when the left-hand sequence was randomized (L_{rand} and LR_{rand}), all $t(23) > 2.58$, all $p \leq .05$. When the right-hand sequence was randomized (R_{rand}), there were also significant left-hand RT costs, $t(23) = 1.89$, $p \leq .05$, but, numerically, left-hand error benefits, which were not significant, however, $t(23) = -1.70$, $p \leq .103$ (two-tailed, because the effect is opposite the predicted direction). Right-hand RT and error costs were significant when the right-hand sequence was randomized (R_{rand} and LR_{rand}), all $t(23) > 2.46$, all $p \leq .05$, but not when the left-hand sequence was randomized (L_{rand}), both $t(23) < 1.34$.

This pattern of hand-related costs evident both in RT costs and in error costs expressed itself in significant Hand × Test Block interactions, both $F(2, 46) > 8.61$, both $p \leq .001$, both $\eta_p^2 > .271$. The significant main effects Test Block, both $F(2, 46) > 6.06$, both $p \leq .005$, both $\eta_p^2 > .208$, are artifacts of averaging across both hands in test blocks in which costs occurred for both hands versus test blocks in which costs occurred for one hand but not the other. The main effects Hand were not significant, both $F(1, 23) < 0.81$, both $\eta_p^2 < .035$.

In order to unpack the significant interactions, separate analyses were computed for left-hand and for right-hand data. These analyses revealed significant main effects Test Block both for left-hand and for right-hand RT as well as error costs, all $F(2, 46) > 5.45$, all $p \leq .01$, all $\eta_p^2 > .192$. Pairwise comparisons revealed that left-hand RT costs differed neither between test blocks L_{rand} and LR_{rand}, $t(23) = 1.78$, $p \leq .132$, nor between test blocks L_{rand} and R_{rand}, $t(23) = 1.98$, $p \leq .09$, but they were significantly higher in test block LR_{rand} than in test block R_{rand}, $t(23) = 3.57$, $p \leq .005$. Left-hand error costs did not differ significantly between test blocks L_{rand} and LR_{rand}, $t(23) = 0.59$, but they were significantly higher in those test blocks than in test block R_{rand}, both $t(23) > 3.67$, both $p \leq .005$. Right-hand RT costs did not differ between test blocks R_{rand} and LR_{rand}, $t(23) = 0.79$, but they were significantly higher in these test blocks than in test block L_{rand}, both $t(23) > 2.93$, both $p \leq .05$. Right-hand error costs differed neither between test blocks R_{rand} and LR_{rand}, $t(23) = 1.50$, $p \leq .222$, nor between test blocks L_{rand} and R_{rand}, $t(23) = 1.70$, $p \leq .154$, but they were significantly higher in test block LR_{rand} than in test block L_{rand}, $t(23) = 3.49$, $p \leq .005$.

Transfer Probes: RT and Error Costs. Significant left-hand and right-hand RT costs were observed in both transfer blocks L_{trans} and R_{trans}, all $t(23) > 4.01$, all $p \leq .001$. These did not differ from RT costs in test block LR_{rand}, $F(2, 46) = 0.21$, $\eta_p^2 = .009$. Notably, in contrast to results from the analysis of test blocks L_{rand}, R_{rand}, and LR_{rand}, there was no significant Hand × Test Block interaction, $F(2, 46) = 0.23$, $\eta_p^2 = .010$, that is, no indication of a pattern of RT costs specific to one hand but not the other. The main effect Hand was not significant either, $F(1, 23) = 0.59$, $\eta_p^2 = .025$.

Transfer block error costs were significant for the right hand, both $t(23) > 1.95$, both $p \leq .032$, but not for the left hand, both $t(23) < 1.70$, both $p \leq .104$. An analysis of variance analogous to that on RT costs revealed no significant main effects or interactions, all $F < 1.49$, all $\eta_p^2 < .061$.

Free Recall. Participants' performance in the post-experimental sequence recall task was scored as described for Experiment 1. In order to split the sample, participants were considered as possessing noticeable explicit sequence knowledge if either the 5-element or the 6-element sequences recalled by them contained 3 or more triples also appearing in the fixed 5-element or 6-element sequence, respectively. According to this operational definition, 10 participants possessed noticeable explicit knowledge of the two sequences: 3 participants for the 6-element sequence, 5 participant for the 5-element sequence, and 2 participants for both sequences. None recalled either of the two sequences completely. The participants with noticeable explicit sequence knowledge produced a mean number of 2.80 triples (out of 6; *SD* = 1.40) from the 6-element sequence and a mean number of 2.90 triples (out of 5; *SD* = 1.79) from the 5-element sequence. The remaining 14 participants produced a mean number of 1.64 triples (out of 6; *SD* = 0.63) from the 6-element sequence and a mean number of 1.29 triples (out of 5; *SD* = 0.83) from the 5-element sequence.

The Role of Explicit Sequence Knowledge. The pattern of significant RT and error costs observed in the sub-sample of participants possessing little explicit sequence knowledge (see Figure 9B) was essentially identical to that reported for the full sample. However, not all main effects and pairwise comparisons were significant: this was the case in particular for right-hand RT and error cost data.

4.1.3 Discussion

In a slight variation of the standard SRT task participants responded alternately with a finger of the left hand and a finger of the right hand to spatial stimuli. The stimuli requiring a left-hand response appeared in a repeating sequence independently of the stimuli requiring a right-hand response which followed another uncorrelated repeating sequence. Together these two interleaved hand-related sequences established a compound sequence spanning both hands.

When randomizing one of the two hand-related sequences while retaining the other, performance deteriorated only for that hand which lost its sequence whereas performance with the other hand did not suffer. In other words, responding with a hand to the sequence practiced with this hand is unaffected by whether responding with the other hand proceeds according to the sequence practiced with that hand or to some random sequence. This pattern of higher costs for a hand upon randomization of its sequence compared to randomization of the other hand's sequence was unequivocal for the left hand in error costs (but not in RT costs) and for the right hand in RT costs (but not in error costs). The finding of left-hand RT costs in test block R_{rand} was most likely due to a speed-accuracy trade-off and does not genuinely reflect integrated learning of the compound sequence as there was a compensatory tendency for left-hand error benefits in the same test block. Taken together, the pattern of randomization costs suggests that after extensive practice the two hand-related sequences are learned and represented independently of one another.

Notably, this pattern of RT and error costs would not have come about if integrated learning of the compound sequence had taken place. Such integrated learning would have entailed learning of between-hand regularities which are destroyed even when only every other stimulus from the compound sequence is replaced with a random stimulus as is the case when one of the two hand-related sequences is randomized while the other is retained. In contrast, within-hand regularities are unaffected by changes to the respective other hand-related sequence. This observed data pattern did not appear to be due to explicit sequence learning.

There were no benefits of executing the transferred sequence with the hand with which the other sequence had been practiced relative to executing a random sequence. Instead, performance deteriorated when executing the transferred sequence just like it did when executing a random sequence. This finding suggests that the independently acquired sequence knowledge is represented in a hand-specific manner that does not allow for intermanual transfer. This conclusion is consistent with results from Experiment 1 and, in particular, Experiment 2, indicating that in the simultaneous bimanual-bisequential SRT task transferable sequence knowledge was acquired only when separate stimuli for the hand-related sequences were present, so that separate S-S or R-S learning was possible, but not when there was only one imperative stimulus indicating both responses. Similarly, because there is only one imperative stimulus on each trial in the alternating bimanual-bisequential SRT task, separate S-S or R-S learning is not likely to have occurred in Experiment 3 either.

Instead of concluding that independent learning of the two hand-related sequences might reflect the operation of separate sequence learning modules for the two hands, one might argue that the sequence learning system might simply have acquired the simplest regularities present which happened to be the short sequences assigned in a hand-related manner to the two hands. The compound sequence established by the two hand-related sequences was considerably longer and more complex and indeed there were no indications of any integrated learning of this compound sequence. This alternative explanation was tested in Experiment 4 by investigating independent learning of correlated hand-related sequences.

4.2 Experiment 4

The major change made in Experiment 4 compared to Experiment 3 was that two hand-related sequences were chosen which are equal in length. Specifically, two correlated second-order conditional sequences established a compound sequence which is similar to its constituent sequences in terms of statistical structure as it is also a second-order conditional sequence. The conditions for integrated learning are further put on par with the conditions for independent learning because the extent of practice is the same for the compound and its constituent sequences: As a result of the hand-related sequences being interleaved, every single repetition of the hand-related sequences is tantamount to a single repetition of the compound sequence. Therefore, if the sequence learning system is simply parsimonious, there should be only integrated learning of the compound sequence and no independent learning of the hand-related sequences. If, however, separate sequence learning modules for the two hands do exist and operate there should be evidence for at least some degree of independent learning of the two hand-related sequences in addition to integrated learning of the compound sequence. Integrated learning of the compound sequence is more likely to occur than in Experiment 3, because the compound sequence in Experiment 4 is much shorter and considerably less complex than the compound sequence in Experiment 3. Test blocks were inserted in session 2 of 3 as well as at the end of session 3, in order to explore whether integrated learning of the compound sequence might develop faster (i.e., after less practice) than independent learning of the constituent hand-related sequences.

4.2.1 Method

Experiment 4 was very similar to Experiment 3 in several respects. Therefore, only the differences between the two experiments are described here.

Participants. A total of 16 individuals (mean age 23 years) volunteered to participate in Experiment 2 in partial fulfillment of course requirements or for payment of €24. Fourteen participants reported to be predominantly right-handed, 1 professed to be ambidextrous, and 1 declared to be predominantly left-handed.

Task and Design. The task was the same as in Experiment 3. Also, the same types of randomization test blocks were implemented. An additional test block was introduced which was also suited to investigating independent versus integrated sequence learning. In this test block, the two hand-related sequences were shifted against each other (LR_{shift}; cf. Schmidtke & Heuer, 1997) so that the position of one sequence (e.g., _X_Y_Z_…) relative to the other sequence (e.g., A_B_C_…) lagged one element behind the relative position as practiced in regular blocks (i.e., AYBZCX… instead of AXBYCZ…). In this way, between-hand regularities are destroyed while within-hand regularities remain intact. As a consequence, performance in such a shift block should not suffer if the two hand-related sequences are learned entirely independently of one another. In contrast, to the extent that integrated learning of the compound sequence occurs which pertains to between-hand regularities, performance should deteriorate in such a shift block.

Apparatus and Materials. Stimulus presentation and response registration was controlled by the E-Prime software package (Schneider et al., 2002). Participants used 8 horizontally aligned keys for responding which were connected to the serial port of the computer via the Psychology Software Tools' (PST) Serial Response Box Model 200a. Stimulus presentation was essentially identical to Experiment 3 except that – instead of 6 – there were 8 horizontally aligned locations on the screen each marked by a line. The 8 keys were assigned from left to right to 8 lines (locations) on the screen. The keys in turn were assigned from left to right to the little, ring, middle, and index finger of the left hand and the index, middle, ring, and little finger of the right hand.

During training, the imperative stimuli appearing in the left-hand side locations (L1, L2, L3, L4) followed a repeating sequence independently of stimuli in the right-hand side locations (R1, R2, R3, R4), which appeared according to a different repeating sequence. Two 8-element sequences were used (Sequence 8A: 14232134; Sequence 8B: 31342124) which together establish a compound 16-element sequence (L1 R3 L4 R1 L2 R3 L3 R4 L2 R2 L1 R1 L3 R2 L4 R4). Although the compound sequence is (a) defined on twice as many positions and is (b) twice as long as its constituent sequences, the 16-element sequence and the 8-element sequences are quite similar in terms of statistical structure: None contains unique transitions (i.e., for each element in the sequence there are two potential successor elements). Instead, all are second-order conditional sequences.

Pseudo-random sequences were constructed according to the same constraints described for Experiment 3, taking into account that each block comprised 128 trials (64 with the left hand and 64 with the right hand). Out of the total of 62 triples contained in each of the pseudo-random sequences selected to replace sequence 8A, either 8, 10, or 15 triples matched one of the 8 triples contained in sequence 8A. Similarly, each of those pseudo-random sequences replacing the sequence 8B contained either 8, 10, 18, or 22 triples (out of a total of 62) matching one of the 8 triples in sequence 8B. No pseudo-random sequences were needed for LR_{shift} test blocks in which – compared to no-shift blocks – sequence 8B lagged one element behind sequence 8A. In order for the shift blocks to constitute the strongest possible test of independent versus integrated sequence learning, sequences 8A and 8B were constructed in such a way that the compound sequence resulting from shifting the hand-related sequences against each other contains no triple that also occurs in the compound sequence in regular unshifted blocks. In contrast, there were chance similarities between the regular unshifted compound sequence and the compound sequences resulting when randomizing both hand-related sequences: the latter contained either 28 or 29 triples (out of a total of 126) matching one of the 16 triples in the former. Therefore, the comparison between test blocks LR_{shift} and LR_{rand} might have been biased against detecting independent sequence learning (lower RTs in LR_{shift} than in LR_{rand}). The compound sequences resulting in those test blocks, in which only one of the sequences was replaced with a pseudo-random sequence while the other was retained, contained between 31 and 33 triples matching triples from the regular unshifted compound sequence, while transfer blocks contained either 23 or 24 such matching triples.

Procedure. The assignment of sequences 8A and 8B to the left and the right hand was counterbalanced across participants. The experiment was conducted in three sessions each comprising 22 blocks. The sessions were scheduled for different days with a maximum of two days between any two sessions (all but two participants completed the experiment on three consecutive days). Session 1 started with a warm-up block in which pseudo-random sequences were presented for both hands, followed by 21 fixed-sequence blocks. Except for the test blocks described below all session 2 and session 3 blocks were fixed-sequence blocks. Beginning with the 4th block in session 2 and with the 11th block in session 3, four test blocks (L_{rand}, R_{rand}, LR_{rand}, LR_{shift}) alternated with four fixed-sequence blocks. The order of presentation of these test blocks was counterbalanced across participants with the additional constraint that none of the participants saw the same order of test blocks in sessions 2 and 3. Session 3 blocks 19 and 21 were test blocks of the L_{trans} and R_{trans} type which were also embedded in fixed-sequence blocks and the order of which was also counterbalanced across participants independently of the counterbalancing of the previous four test blocks.

Each block comprised 128 trials (64 with the left hand and 64 with the right hand), so that participants completed 192 and 392 repetitions of sequences 8A and 8B as well as of the compound 16-element sequence prior to test blocks in session 2 and session 3, respectively (not counting sequence repetitions in session 2 test blocks L_{rand}, R_{rand} , and LR_{shift}). The response-stimulus interval was 120 ms.

4.2.2 *Results*

RTs from error trials (4.9%) as well as outlier RTs (1.6%) were excluded from analysis. The means of the individual median RTs are shown in Figure 10 for each block across the experiment. RT costs and error costs in randomization and transfer blocks were computed as described for Experiment 3. None of the error cost variables differed significantly from a normal distribution, all Kolmogorov–Smirnov *Z*s between 0.36 and 0.86, all $p > .453$. In keeping with the order of presentation of results as established for the previous experiments, data from randomization test blocks will be analyzed first, followed by data from transfer blocks, before data from the newly introduced shift blocks are analyzed. Also consistent with previous experiments, analyses will focus on comparing costs in randomization and transfer blocks in a within-hands manner rather than in a between-hands manner. The former type of comparison appears to be more sensitive for detecting hand-related sequence learning than the latter when considering that hand-related sequence learning as reflected in randomization costs might be not be equally pronounced for both hands.

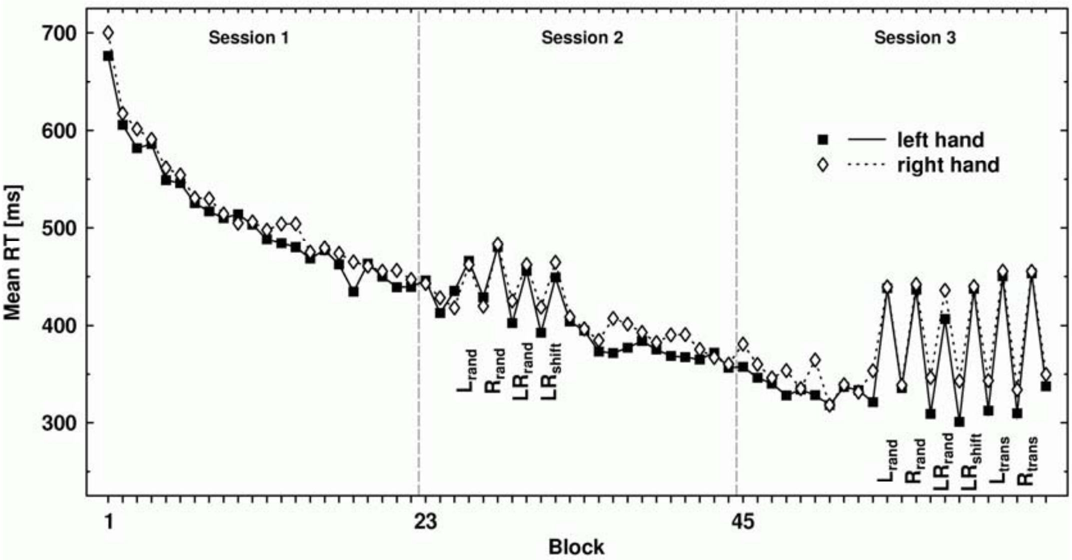


Figure 10. Means of individual median RTs in Experiment 4 separately for the left and the right hand. For presentation purposes, test blocks are ordered in a consistent manner; in reality, the order of test blocks was counterbalanced across participants.

Randomization Probes: RT Costs. There were significant left-hand and right-hand RT costs in all test blocks (L_{rand}, R_{rand}, and LR_{rand}) both in Session 2, all $t(15) > 2.95$, all $p \leq .01$, and in Session 3, all $t(15) > 5.43$, all $p \leq .001$ (see Figure 11).

In session 2, RT costs differed neither between Test Blocks nor between Hands, both $F < 1.38$, both $\eta_p^2 < .084$, but the Hand (left, right) × Test Block (L_{rand}, R_{rand}, LR_{rand}) interaction was significant, $F(2, 30) = 4.50$, $p \leq .05$, $\eta_p^2 = .231$. Separate analyses for left-hand and right-hand data revealed that there was a tendency for left-hand RT costs to differ between test blocks as indicated by a marginally significant main effect, $F(2, 30) = 3.22$, $p \leq .054$, $\eta_p^2 = .177$, but none of the pairwise comparisons were significant, all $t(14) < 2.21$, no $p \leq .065$. Right-hand RT costs did not differ significantly between test blocks, $F(2, 30) = 1.58$, $\eta_p^2 = .095$.

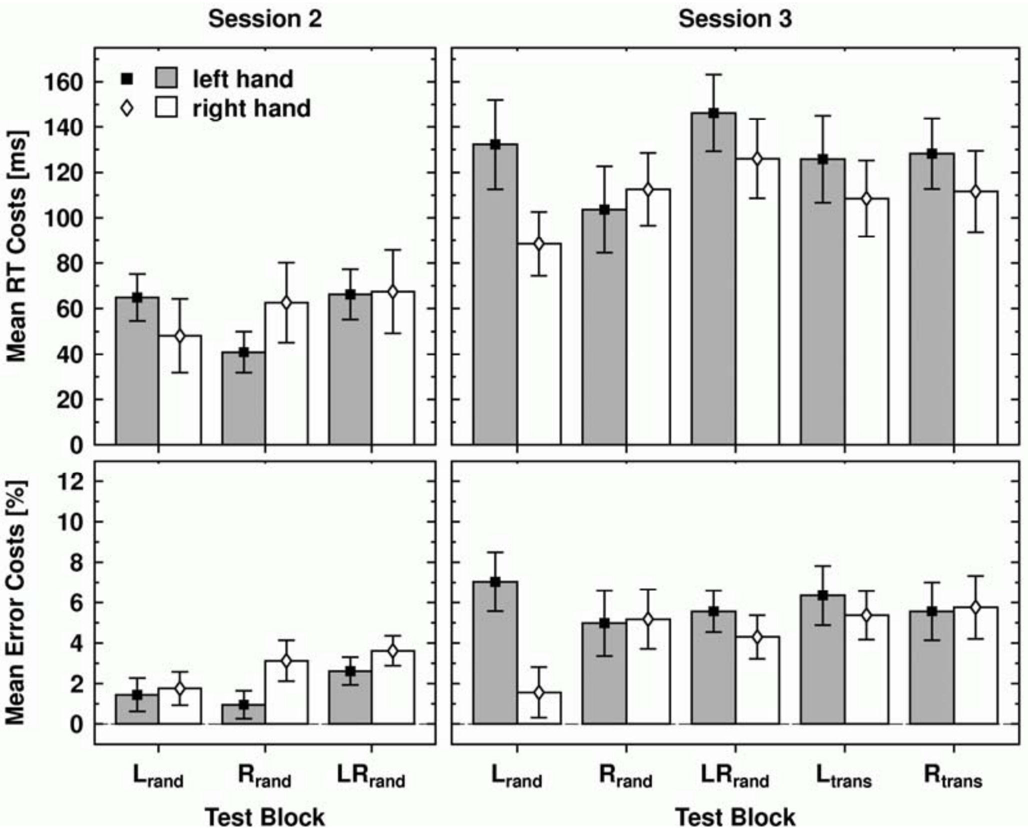


Figure 11. Mean RT and error costs in each of the test blocks in session 2 and session 3 of Experiment 4 separately for the left and the right hand. Error bars represent standard errors of the means.

In session 3, the main effect Hand was again not significant, $F(1, 15) = 1.84$, $\eta_p^2 = .109$. However, the main effect Test Block was significant, $F(2, 30) = 14.69$, $p \leq .001$, $\eta_p^2 = .495$, as was the Hand × Test Block interaction, $F(2, 30) = 10.85$, $p \leq .001$, $\eta_p^2 = .420$. Both left-hand

and right-hand RT costs differed significantly between test blocks, both $F(2, 30) > 10.98$, both $p \leq .001$, both $\eta_p^2 > .423$. Left-hand RT costs did not differ significantly between test blocks L_{rand} and LR_{rand}, $t(15) = 1.85$, $p \leq .127$, but were significantly higher in these test blocks than in test block R_{rand}, both $t(15) > 3.88$, both $p \leq .005$. Unlike left-hand RT costs, right-hand RT costs did not differ significantly between test blocks R_{rand} and LR_{rand}, $t(15) = 2.13$, $p \leq .076$, but were significantly higher in these test blocks than in test block L_{rand}, both $t(15) > 2.73$, both $p \leq .05$.

Although this pattern of hand-specific RT costs was statistically significant in session 3 but not in session 2, the corresponding three-way Session × Hand × Test Block interaction was not significant in the overall ANOVA, $F(2, 30) = 0.34$, $\eta_p^2 = .022$. The analysis showed, however, that RT costs were significantly higher in session 3 ($M = 118.2$ ms; $SE = 15.2$) than in session 2 ($M = 58.4$ ms; $SE = 11.3$), $F(1, 15) = 60.58$, $p \leq .001$, $\eta_p^2 = .802$. Also, there was a significant main effect Test Block, $F(2, 30) = 7.60$, $p \leq .005$, $\eta_p^2 = .336$, as well as a significant Hand × Test Block interaction, $F(2, 30) = 14.23$, $p \leq .001$, $\eta_p^2 = .487$. No other main effects or interactions were significant, all $F < 1.42$, all $\eta_p^2 < .087$. The Hand × Test Block interaction reflected a pattern of hand-specific RT costs as described above for session 3, with RT/error costs for each hand significantly higher when the respective hand's sequence was randomized than when it was maintained while the other hand's sequence was randomized.

Randomization Probes: Error Costs. In session 2, left-hand error costs were significant in test block LR_{rand}, $t(15) = 3.83$, $p \leq .005$, but only marginally significant in test block L_{rand}, $t(15) = 1.74$, $p \leq .052$, and not significant in test block R_{rand}, $t(15) = 1.39$, $p \leq .093$. In contrast, right-hand error costs were significant in all test blocks, all $t(15) > 2.14$, all $p \leq .05$. A Hand × Test Block ANOVA revealed a significant main effect Test Block, $F(2, 30) = 5.66$, $p \leq .01$, $\eta_p^2 = .274$, indicating that error costs in test block LR_{rand} were significantly higher than error costs in test blocks L_{rand} and R_{rand}, both $t(15) > 2.62$, both $p \leq .05$, whereas error costs did not differ between test blocks L_{rand} and R_{rand}, $t(15) = 0.86$. Neither the main effect Hand nor the Hand × Test Block interaction were significant, both $F < 2.44$, both $\eta_p^2 < .140$.

In session 3, significant left-hand error costs were observed in all test blocks, all $t(15) > 3.08$, all $p \leq .01$, whereas right-hand error costs were significant in test blocks R_{rand} and LR_{rand}, both $t(15) > 3.51$, both $p \leq .005$, but not in test block L_{rand}, $t(15) = 1.25$, $p \leq .115$. A Hand × Test Block ANOVA revealed a significant Hand × Test Block interaction, $F(2, 30) = 5.81$, $p \leq .01$, $\eta_p^2 = .279$. Neither of the two main effects were significant, both $F < 2.19$, both $\eta_p^2 < .128$. The significant interaction reflected that left-hand error costs did not differ significantly between test blocks, $F(2, 30) = 1.81$, $p \leq .181$, $\eta^2_p = .108$, whereas right-hand error costs did differ significantly between test blocks, $F(2, 30) = 4.25$, $p \leq .05$, $\eta^2_p = .221$, such that right-hand error costs differed significantly between test blocks L_{rand} and R_{rand}, $t(15) = 2.95$, $p \leq .01$, but neither between test blocks L_{rand} and LR_{rand}, $t(15) = 1.81$, $p \leq .136$, nor between test blocks R_{rand} and LR_{rand}, $t(15) = 0.80$.

An overall Session × Hand × Test Block ANOVA showed that error costs were generally higher in session 3 (M = 4.8%; SD = 0.9%) than in session 2 (M = 2.3%; SD = 0.5%), $F(1, 15) = 11.50$, $p \leq .005$, $\eta^2_p = .434$. Also, the interaction between the factors Hand and Test Block was significant, $F(2, 30) = 5.30$, $p \leq .05$, $\eta^2_p = .261$, as was the interaction between the factors Session and Hand, $F(1, 15) = 4.80$, $p \leq .05$, $\eta^2_p = .243$. No other main effects or interaction were significant, all $F < 1.99$, all $\eta^2_p < .118$.

The Hand × Test Block interaction in this overall analysis reflected that left-hand error costs did not differ significantly between test blocks, $F(2, 30) = 1.91$, $\eta^2_p = .113$, whereas right-hand error costs did differ significantly between test blocks, $F(2, 30) = 5.01$, $p \leq .05$, $\eta^2_p = .251$. Specifically, right-hand error costs did not differ significantly between test blocks R_{rand} and LR_{rand}, $t(15) = 0.26$, but they were significantly higher in these test blocks than in test block L_{rand}, both $t(15) > 2.54$, both $p \leq .05$. The Hand × Session interaction was due to error costs in session 2 being numerically higher for the right hand than for the left hand, while error costs in session 3 were numerically higher for the left hand than for the right hand. However, neither difference was significant as a main effect in separate ANOVAS for the two sessions, as reported above.

Transfer Probes: RT and Error Costs. Significant left-hand and right-hand RT costs as well as error costs were observed in both transfer blocks L_{trans} and R_{trans}, all $t(15) > 3.70$, all $p \leq .005$. In a Hand (left, right) × Test Block (LR_{rand}, L_{trans}, R_{trans}) ANOVA on RT costs the main effect Test Block missed significance, $F(2, 30) = 3.36$, $p \leq .067$, $\eta^2_p = .183$, $\varepsilon_{GG} = .721$. Additionally confirming this lack of an effect of the transfer manipulation, none of the pairwise comparisons between test blocks computed separately for each hand were significant, all $t(15) < 2.08$, no $p \leq .083$. Neither the main effect Hand nor the Hand × Test Block interaction was significant, both $F < 2.17$, both $\eta^2_p < .127$. An analogous ANOVA on error costs revealed no significant main effects or interactions, all $F < 0.49$, all $\eta^2_p < .032$.

Shift Probe RTs. An ANOVA with repeated measures on the factors Session (session 2, session 3), Hand (left, right), and Block Structure (test block LR_{rand}, test block LR_{shift}, baseline fixed sequence blocks LR_{base}) on absolute median RTs revealed significant main effects Session, $F(1, 15) = 63.16, p \leq .001, \eta_p^2 = .808$, and Block Structure, $F(2, 30) = 24.78, p \leq .001, \eta_p^2 = .623$, which were involved in a significant two-way interaction, $F(2, 30) = 25.10, p \leq .001, \eta_p^2 = .626$. No other main effects and interactions were significant, all $F < 1.29$, all $\eta_p^2 < .080$.

The significant Session × Block Structure interaction reflected that the main effect Block Structure was less pronounced in session 2, $F(2, 30) = 12.04, p \leq .001, \eta_p^2 = .445$, than in session 3, $F(2, 30) = 33.29, p \leq .001, \eta_p^2 = .689$. All pairwise comparisons between test blocks LR_{rand}, LR_{shift}, and LR_{fixed} were significant in session 2, all $t(15) > 2.41$, all $p \leq .05$, and in session 3, all $t(15) > 3.86$, all $p \leq .005$, with RTs in test blocks LR_{shift} falling between higher RTs in test block LR_{rand} and lower RTs in test block LR_{fixed} (see Figure 12A).

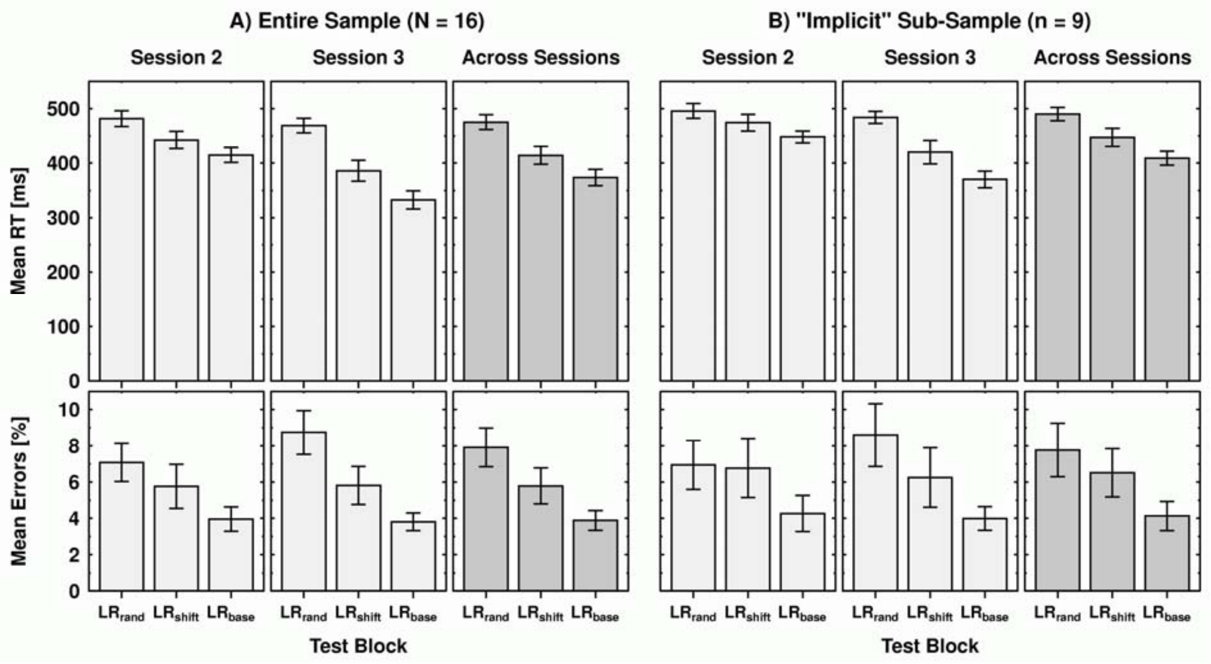


Figure 12. Means of individual median RTs in randomization block LR_{rand}, in shift block LR_{shift}, and in regular baseline blocks LR_{base} in Experiment 4 separately for and across both sessions; separately for the entire sample (A) and for the sub-sample of participants who possessed only little explicit knowledge of the sequences (B). Error bars represent standard errors of the means.

One might argue that the finding of faster RTs in test block LR_{shift} than in test block LR_{rand} might be due to within-block learning of the new compound sequence constituted by the shifted hand-related sequences. Contrary to what would be expected if that was the case, however, RTs in test block LR_{shift} were not significantly faster in the second block half than in the first block half, either in session 2, $F(1, 15) = 0.19, \eta_p^2 = .012$, or in session 3, $F(1, 15) = 0.70, \eta_p^2 = .044$, or across sessions, $F(1, 15) = 0.54, \eta_p^2 = .035$.

Shift Probe Errors. None of the absolute relative error rate variables differed significantly from a normal distribution, all Kolmogorov–Smirnov *Z*s between 0.46 and 1.11, all $p >$ .176. An ANOVA on relative error frequencies analogous to that on median RTs revealed a significant main effect Block Structure, $F(2, 30) = 30.22$, $p \leq .001$, $\eta_p^2 = .668$, indicating that error frequency was significantly higher in block LR_{rand} than in blocks LR_{shift} and LR_{fixed}, both $t(15) > 5.01$, both $p \leq .001$, and that error frequency in block LR_{shift} was significantly higher than in block LR_{fixed}, $t(15) = 3.61$, $p \leq .005$. Among the other main effects and interactions, the Session × Block Structure interaction came closest to but did not reach significance, $F(2, 30) = 2.13$, $p \leq .137$, $\eta_p^2 = .124$. No other main effects and interactions were significant, all $F <$ 1.09, all $\eta_p^2 < .068$.

Again, contrary to what would be expected if within-block learning had taken place, error rates in test block LR_{shift} were not significantly reduced in the second block half compared to the first block half, either in session 2, $F(1, 15) < 0.01$, $\eta_p^2 < .001$, or in session 3, $F(1, 15) = 1.19$, $\eta_p^2 = .073$, or across sessions, $F(1, 15) = 0.73$, $\eta_p^2 = .046$.

Free Recall. Participants' recall performance was scored according to the procedure described for Experiment 3. In order to split the sample, participants were considered as possessing noticeable explicit sequence knowledge if they produced 4 or more triples from either of the two 8-element sequences. According to this operational definition, 6 participants possessed noticeable explicit knowledge of sequence 8A, and 1 participant possessed noticeable explicit knowledge of sequence 8B. None recalled either of the two sequences completely. The participants with noticeable explicit sequence knowledge produced a mean number of 5.00 triples (out of 8; *SD* = 2.08) from sequence 8A and a mean number of 1.86 corresponding triples (out of 8; *SD* = 1.07) from sequence 8B. The remaining 9 participants produced a mean number of 1.56 corresponding triples (out of 8; *SD* = 1.13) from sequence 8A and a mean number of 1.67 corresponding triples (out of 8; *SD* = 1.12) from sequence 8B.

The Role of Explicit Sequence Knowledge. Again, analyses of RT and error data restricted to those participants possessing little explicit sequence knowledge (see Figures 13, 12B) yielded largely the same pattern of results as reported for the full sample. Indications for independent learning of the right-hand sequence were weak in randomization probes, but independent learning of the hand-related sequences was confirmed in shift probes.

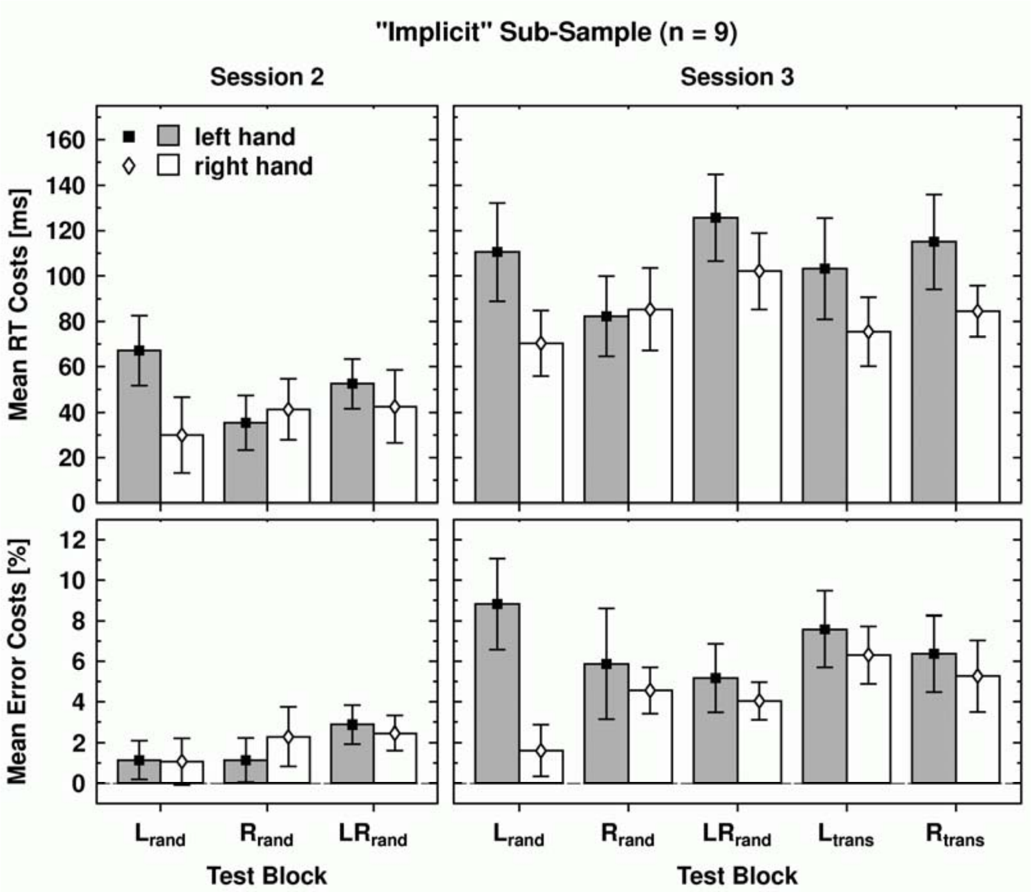


Figure 13. Mean RT and error costs in each of the test blocks in session 2 and session 3 of Experiment 4 separately for the left and the right hand. Data from the sub-sample of participants who possessed little explicit knowledge about the sequences. Error bars represent standard errors of the means.

4.2.3 Discussion

As in Experiment 3, participants in Experiment 4 responded alternately with the left and the right hand to spatial stimuli; again, left-hand and right-hand stimuli appeared in different repeating sequences. Unlike Experiment 3, these two hand-related sequences were equally long and therefore correlated. Specifically, two interleaved hand-related second-order conditional sequences of length 8 established a compound second-order conditional sequence of length 16 spanning both hands. In contrast to Experiment 3, responding with both hands slowed down relative to baseline blocks irrespective of whether only one or both of the two hand-related sequences were randomized. This finding clearly indicates integrated learning of the compound sequence. Moreover, the amount of acquired integrated sequence knowledge increased with practice (i.e., from session 2 to session 3).

However, there was also evidence that – in addition to integrated learning – the two hand-related sequences were to some degree learned independently of one another: Speed of responding with the left hand deteriorated more pronouncedly when the left hand lost its sequence than when it retained its sequence while the other hand lost its sequence. The same is true for the right hand. This pattern of hand-related performance decrements was significant only in session 3, but not in session 2. Effects in terms of error frequency were less clear-cut, providing some evidence for integrated as well as for independent sequence learning. In any case, it can be ruled out that the pattern of RT costs indicating independent learning was due to a speed-accuracy trade-off.

Further evidence for partly independent learning of hand-related sequences comes from test blocks in which the two sequences were shifted relative to each other so that all within-hand regularities are retained but all between-hand regularities are abolished, which essentially define the compound sequence. These shift blocks resulted in a significant performance decrement relative to baseline blocks in session 3, but not in session 2. In both sessions, however, participants responded faster in shift blocks than in blocks in which the compound sequence is destroyed by randomizing both hand-related sequences (LR_{rand}). This benefit for shift blocks (a) emerged although the compound sequence newly formed by shifting the hand-related sequences had not a single triple in common with the practiced compound sequence, whereas some such corresponding triples occurred by chance (i.e., as a result of randomization) in test blocks LR_{rand}, and (b) did not appear to have resulted from within-block learning. Participants evidently benefited from the within-hand regularities still present in shift blocks even though between-hand regularities were altered. At the same time, the fact that performance in shift blocks was worse than in baseline blocks in session 3 indicates that sequence learning was not entirely independent but that integrated sequence learning had also occurred. Again, the observed data pattern did not appear to be due to explicit sequence learning.

As for the issue of possibly different time courses for integrated and independent learning, results from randomization blocks seem to suggest that integrated learning of the compound sequence might develop more quickly than independent learning of the constituent hand-related sequences, whereas results from shift blocks indicate the opposite. As the respective statistical interaction was significant only in the latter but not in the former analysis, it might seem as if the case for faster independent than integrated learning is somewhat stronger than the case for faster integrated than independent learning, but the data are really not conclusive. Further investigation is necessary in order to resolve this issue.

Even though the two hand-related sequences appeared to have been learned partly independently, neither response times nor response accuracy provided any reliable indications of intermanual transfer. This lack of intermanual transfer is consistent with findings from Experiment 3 and the single-stimulus condition of Experiment 2.

In sum, the results of Experiment 4 confirm those of Experiment 3 inasmuch as they indicate partly independent learning of hand-related sequences under conditions of alternating responding and thus lend further support to the idea that separate sequence learning modules might exist for the left and the right hand.

4.3 Experiment 5

Another way of investigating whether separate sequence learning modules exist for the left and the right hand was adopted in Experiment 5, namely, comparing (a) sequence learning under conditions of practicing a sequence solely with fingers of one hand and (b) sequence learning under conditions of practicing the same sequence with fingers of both hands. In order to keep conditions as similar as possible to Experiments 3 and 4, sequence learning with (a) fingers of one hand (within-hands assignment) was compared to sequence learning with (b) fingers of both hands (across-hands assignment) in the presence of random stimuli for the respective other fingers.

Stimuli from the fixed sequence appeared alternately with random stimuli so that every other stimulus and, thus, every other response was part of a repeating sequence. That sequence learning under such conditions is possible, has been confirmed by J. H. Howard and Howard (1997; see also J. H. Howard, Howard, Dennis, Yankovich, & Vaidya, 2004; D. V. Howard et al., 2004; Japikse et al., 2003): In what they termed alternating SRT (ASRT) task, sequence trials alternated with random trials just like they did here. In contrast to this experiment, however, sequence stimuli appeared in the same locations as random stimuli and participants used the same fingers on the same keys for responding both to sequence stimuli and to random stimuli.

If the sequence learning system was simply associating alternating stimuli/responses irrespective of the effector used for responding, sequence learning in the within-hands assignment should not differ from sequence learning in the across-hands assignment. In contrast, if forming associations between stimuli/responses pertaining to fingers of the same hand is privileged, sequence learning should be better (i.e., faster and/or more pronounced) in the within-hands assignment than in the across-hands assignment and this finding would qualify as an expression of the operation of a separate sequence learning modules for each hand.

4.3.1 Method

Experiment 5 was similar to Experiment 4 especially in terms of equipment used. Therefore, only the differences between the two experiments are described here.

Participants. A total of 32 individuals (mean age 22.3 years) volunteered to participate in partial fulfillment of course requirements or for payment of €18. Twenty-seven participants reported to be predominantly right-handed, 3 declared to be ambidextrous, and the remaining 2 were predominantly left-handed.

Task and Design. The task was very similar to Experiments 3 and 4: Participants responded to the location of a single stimulus by pressing the corresponding key with the assigned finger. Unbeknownst to participants, stimuli from a fixed sequence appeared alternately with random stimuli. Unlike Experiments 3 and 4, there was only one type of test block, in which the fixed sequence was replaced with a random sequence so that all stimuli/responses were random.

Apparatus and Materials. Participants used 8 horizontally aligned keys for responding which were arranged on the tabletop in 2 groups of 4 keys each. Participants used the 4 keys on the left-hand side for responding with the little, ring, middle, and index finger and the 4 keys in the right-hand side for responding with the index, middle, ring, and little finger of the right hand. A barrier placed on the table prevented participants from seeing the keys and their hands during the experiment.

The imperative stimuli were asterisks 9 mm in diameter. There were a total of eight locations in which asterisks could appear each marked by a square black outline (side length 21 mm). The squares were arranged in two rows consisting of four squares each and with a horizontal distance of 6 mm between any two adjacent squares. These two rows overlapped in the center of the screen. The non-overlapping halves of each row were horizontally aligned; the overlapping halves of each row were shifted the same distance upwards and downwards from the center of the screen, respectively, so that a horizontal distance of 12 mm resulted between the vertically aligned two upper and two lower squares (see Figure 14A). This layout can be divided either into a lower left row and an upper right row of squares (imagine a diagonal with negative slope halving the layout) or, alternatively, into an upper left row and a lower right row of four squares each (imagine a diagonal with positive slope halving the layout) (see Figure 14B).

The asterisks in the lower left/right row or in the upper right/left row of squares (referred to henceforth as 1, 2, 3, and 4 from left to right; see also Figure 14C) appeared according to an 8-element second-order conditional sequence (41423213). The asterisks in the other

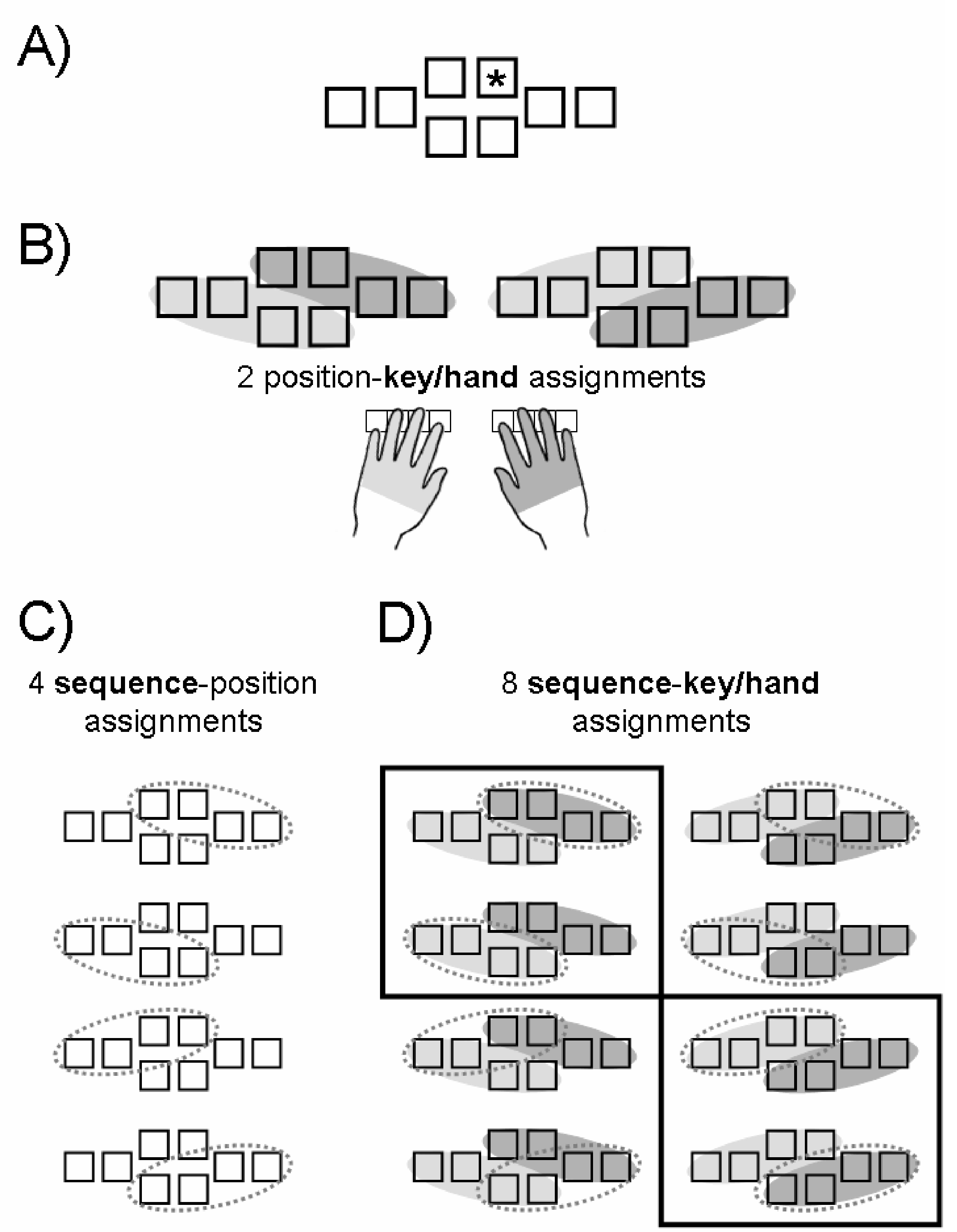


Figure 14. Illustration of (A) the stimulus display in Experiment 5, (B) the two possible assignments of positions to the left and the right group of keys and thus to the left and the right hand, (C) the four possible assignments of the fixed sequence to positions in the stimulus display (‘sequence positions’ are encircled with a dotted line), and finally (D) the within-hands and the across-hands assignments of the fixed sequence to keys and thus fingers of the two hands resulting when fully crossing the assignments depicted in panels B and C (the within-hands assignments are enclosed in boxes).

(i.e., upper right/left or in the lower left/right) row of squares (referred to here as A, B, C, and D from left to right) appeared randomly under the constraint that (a) within each block every position occurred equally often and that (b) each sequence-to-random transition (e.g., 1-A, 1-B, 1-C, 1-D, 2-A, 2-B, …) and each random-to-sequence transition (e.g., A-1, A-2, A-3, A-4, B-1, B-2, …) occurred no less than 7 times and no more than 9 times within each block. These constraints were also adhered to in constructing random sequences for randomization test blocks.

The squares in the left row (either upper left or lower left) were always assigned from left to right to the little, ring, middle, and index finger of the left hand. Likewise, the squares in the right row (either lower right or upper right) were always assigned from left to right to the index, middle, ring, and little finger of the right hand (see Figure 14B). The assignment of the two rows of squares to the two hands either coincided with the assignment of the fixed sequence to the rows of squares or varied orthogonally to it. The resulting assignment of the fixed sequence and the random sequence to the hands is within-hands in the former case and across-hands in the latter case (see Figure 14D). For example, if the assignment of the fingers of the left hand to the squares of the upper left row coincides with the asterisks in the upper left row of squares appearing according to the fixed sequence (which means that the sequence of asterisks on the lower right row is random), participants respond to the fixed sequence with the left hand, while the random sequence is responded to with the right hand (within-hands assignment). In contrast, if the fingers of the left hand are assigned to the upper left row of squares and the fixed sequence is assigned to the upper right row of squares (so that the random sequence is localized in the lower left row of squares), participants respond to the fixed sequence with the middle and index finger of the left hand and the ring and little finger of the right hand, while the random sequence is responded to with the little and ring finger of the left hand and the index and middle finger of the right hand (across-hands assignment). All 4 possible within-hands and all 4 possible across-hands assignments were implemented for an equal number of participants.

Procedure. Participants were tested individually. The experiment was conducted in three sessions scheduled for separate days with a maximum of three days between any two sessions (all but nine participants completed the experiment on three consecutive days). Each session consisted of 22 blocks. Session 1 started with a warm-up block in which all stimuli were random. In all other blocks the stimuli appearing in one row of locations followed the fixed sequence while the stimuli appearing in the other row of locations appeared randomly as described above. Exceptions to this rule were the last but one block in each session which was always a test block in which the fixed sequence was replaced with a random sequence. Each block comprised 128 trials, 64 sequence trials alternating with 64 random trials. It was randomly determined for each block whether it started with a sequence trial or a random trial.

Written instructions were augmented by an illustration similar to Figure 14B. Participants took self-terminated rest periods between blocks and initiated each block by pressing any one of the 8 response keys.

After completing the SRT task in session 3, participants were debriefed about the presence of a fixed repeating sequence for one row of positions on the monitor (and, thus, for one half of the keys and one half of their fingers) and random stimuli for the remaining positions (keys, fingers). Then, they completed a set of post-experimental tasks designed to assess the extent of their explicit sequence knowledge.

When attempting to diagnose explicit knowledge, one is faced with a sensitivity-contamination dilemma (Goschke, 1998): Highly sensitive methods of assessing explicit sequence knowledge are likely to be contaminated by implicit sequence knowledge, whereas relatively pure methods of assessing explicit sequence knowledge are probably afflicted with sub-optimal sensitivity. For example, asking participants to report verbally everything they have noticed about a sequence of stimuli and responses during an SRT experiment will yield a relatively pure assessment of consciously available explicit sequence knowledge, but any explicit knowledge that cannot be verbalized will be left out of the assessment. In contrast, forced choice recognition tasks, for example, are sure to reflect explicit sequence knowledge even if it cannot be verbalized, but this increased sensitivity comes at the price of an increased risk of participants' performance in the task also being influenced by implicit sequence knowledge. The sequence recall task employed in Experiments 1–4 might have yielded rather conservative assessments of the extent of participants' explicit sequence knowledge. In Experiment 5, the assessment of the extent of participants' explicit sequence knowledge was modeled closely after Destrebecqz and Cleeremans (2001; cf. Goschke, 1998) who tackled the sensitivity-contamination dilemma by adapting the process-dissociation procedure proposed by Jacoby (1991).

Participants were instructed to try to generate a sequence which resembles the sequence present in the experiment as much as possible (inclusion instructions). They were informed that no immediate repetitions of the same key occurred in the practiced sequence and asked to avoid such immediate repetitions when generating a sequence. Also, participants were told to use only those keys for which the sequence was present during the experiment. In fact, only those keys accepted input during this generation task. Participants had to generate a sequence consisting of 64 key presses. The task was self-paced. Upon each key press, an asterisk appeared in the corresponding location on the screen providing feedback about the response that was given; that asterisk remained on screen until the next key was pressed. After completing this first part of the generation task, participants were instructed to try to generate a sequence which resembles the practiced sequence as little as possible (exclusion instructions). They were reminded to avoid immediate repetitions of the same key. If participants were allowed to continually press the same key they could completely avoid producing any chunks from the practiced sequence, but that would reveal very little about their actual explicit sequence knowledge. Again, participants had to generate a sequence of 64 key presses.

The logic behind having participants perform the generation task under inclusion and exclusion instructions is the following: Generating chunks from the practiced sequence under inclusion instructions will likely reflect not only explicit but to some degree also some implicit sequence knowledge. In contrast, generating chunks from the practiced sequence under exclusion conditions can only reflect an influence of implicit sequence knowledge on performance because if participants had intentional control over all sequence knowledge they would be able to completely avoid producing any chunks from the practiced sequence. Thus, the extent of a participant's explicit sequence knowledge can be estimated by subtracting that participant's score under exclusion conditions from her/his score under inclusion conditions. To spell out the two extreme cases: If a participant had no intentional control over acquired sequence knowledge, her/his score under exclusion conditions should not differ from that under inclusion conditions, so that a difference score of 0 reflects completely implicit sequence learning. If, on the other hand, a participant had full intentional control over acquired sequence knowledge, her/his score under inclusion conditions should be maximal whereas her/his score under exclusion conditions should be 0, as she/he will be able to avoid producing any chunks from the practiced sequence; thus, a maximal difference score reflects completely explicit sequence knowledge.

4.3.2 Results

RTs from error trials (6.0%) as well as outlier RTs (1.8%) were excluded from analysis. From the remaining data points the median RT was calculated separately for sequence trials and for random trials for each block within each session and for each participant. The means of these median RTs across the experiment are plotted in Figure 15. Likewise, relative error frequency (percent errors, PE) was calculated separately for sequence and random trials for each participant, session, and block. Among the 18 absolute relative error rate variables in Experiment 5 only one (sequence-trial error rates from the randomization block in Session 1) differed significantly from a normal distribution, Kolmogorov–Smirnov $Z = 1.37$, $p = .047$, whereas the remaining variables did not, all Kolmogorov–Smirnov *Z*s between 0.54 and 1.26, all $p > .085$. Again, the Greenhouse-Geisser correction was applied in repeated-measures analyses of variance (ANOVA) whenever necessary.

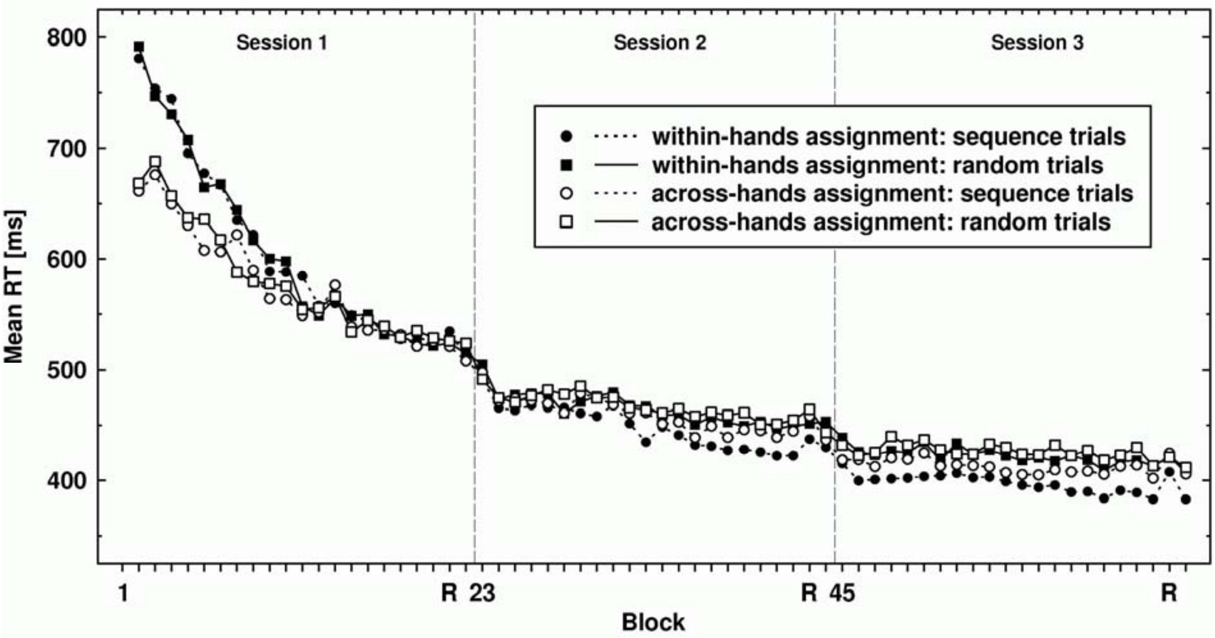


Figure 15. Means of individual median RTs in Experiment 5 separately for sequence and for random trials and separately for the within-hands and the across-hands assignment (R = randomization test block).

Randomization Probes. RTs as well as PEs were analyzed in 3 (Session: 1, 2, 3) × 2 (Trialtype: sequence vs. random) × 2 (Blocktype: baseline vs. randomization test) × 2 (Assignment: within-hands vs. across-hands) mixed-factors ANOVAs with repeated measures on the first three factors. Both analyses revealed several significant main effects and interactions (see Tables 4 and 5) including significant Trialtype × Blocktype interactions. This interaction is critical for the question of whether the sequence is indeed learned independently of the random trials, that is, whether randomization in test blocks leads to costs relative to baseline blocks only on sequence trials but not on random trials. Because the significant Trialtype × Blocktype interaction suggested that this was the case, I proceeded by running separate Session × Blocktype × Assignment ANOVAs for data from sequence trials and data from random trials.

Table 4

Results of the Session (1, 2, 3) × Trialtype (sequence vs. random trials) × Blocktype (baseline vs.randomization block) × Assignment (single-hand vs. hand-distributed) ANOVA on reaction time (RT) data from Experiment 5.

	ANOVA on RTs						
	df1	df2	ε_{GG}	F	p		η_p^2
Assignment	1	30		0.09	.761		.003
Session	2	60	.976	223.79	.000	***	.882
Trialtype	1	30		5.02	.033	*	.143
Blocktype	1	30		32.92	.000	***	.523
S × A	2	60		0.70	.500		.023
T × A	1	30		0.62	.439		.020
B × A	1	30		0.01	.931		.000
S × T	2	60	.955	3.55	.035	*	.106
S × T × A	2	60		4.93	.010	*	.141
S × B	2	60	.836*	3.40	.049	*	.102
S × B × A	2	60		4.60	.014	*	.133
T × B	1	30		4.93	.034	*	.141
T × B × A	1	30		0.45	.509		.015
S × T × B	2	60	.915	0.47	.628		.015
S × T × B × A	2	60		0.33	.717		.011

Note. Significance levels are coded as follows: * indicates $p \leq .05$, ** indicates $p \leq .01$, and *** indicates $p \leq .001$.

Randomization Probes: Random-trial RTs and PEs. RTs on random trials decreased with each session, $F(2, 60) = 156.23$, $p \leq .001$, $\eta_p^2 = .839$ ($M_{S1} = 523.9$ ms, $SE_{S1} = 12.0$; $M_{S2} = 453.7$ ms, $SE_{S2} = 11.4$; $M_{S3} = 415.9$ ms, $SE_{S3} = 8.9$), all pairwise comparisons, $p \leq .001$, and were generally higher in randomization test blocks ($M = 468.1$ ms, $SE = 10.4$) than in baseline blocks ($M = 460.9$ ms, $SE = 10.2$), $F(1, 30) = 6.67$, $p \leq .05$, $\eta_p^2 = .182$. No other main effects or interactions were significant, all $F < 2.32$. These RT costs (see Figure 16A) do not truly reflect sequence learning, however, as there were compensatory PE benefits (i.e., generally lower PEs on random trials in randomization test blocks [$M = 5.3\%$, $SE = 0.6$] than in baseline blocks [$M = 6.5\%$, $SE = 0.6$]; see Figure 16B), $F(1, 30) = 17.78$, $p \leq .001$, $\eta_p^2 = .372$. No other main effects or interactions were significant, all $F < 1.43$.

Table 5
Results of the Session (1, 2, 3) × Trialtype (sequence vs. random trials) × Blocktype (baseline vs.randomization block) × Assignment (single-hand vs. hand-distributed) ANOVA on percent error (PE) data from Experiment 5.

	ANOVA on PEs						
	df1	df2	ε_{GG}	F	p		η^2_p
Assignment	1	30		0.62	.436		.020
Session	2	60	.722***	1.24	.289		.040
Trialtype	1	30		0.47	.499		.015
Blocktype	1	30		2.57	.120		.079
S × A	2	60		0.20	.818		.007
T × A	1	30		4.22	.049	*	.123
B × A	1	30		7.65	.010	*	.203
S × T	2	60	.950	0.28	.757		.009
S × T × A	2	60		1.51	.228		.048
S × B	2	60	.898	5.25	.008	**	.149
S × B × A	2	60		0.09	.916		.003
T × B	1	30		35.86	.000	***	.545
T × B × A	1	30		2.55	.121		.078
S × T × B	2	60	.996	1.18	.315		.038
S × T × B × A	2	60		0.82	.446		.027

Note. Significance levels are coded as follows: * indicates $p \leq .05$, ** indicates $p \leq .01$, and *** indicates $p \leq .001$.

Randomization Probes: Sequence-trial RTs. As for sequence trial RTs, the Session × Blocktype × Assignment ANOVA revealed several significant main effects and interactions (see Table 6) including the three-way interaction. In order to unpack this interaction, separate Blocktype × Assignment ANOVAs were computed for each session. In all three sessions, RTs were higher in randomization test blocks than in baseline blocks, all $F(1, 30) > 7.26$, all $p \leq .05$, all $\eta^2_p > .194$ (see Figure 16C), reflecting that participants had acquired knowledge about the sequence. In session 1, this RT increase was significant in the within-hands assignment, $t(15) = 3.39$, $p \leq .01$, but not in the across-hands assignment, $t(15) = 0.59$. However, the corresponding Blocktype × Assignment interaction missed statistical significance, $F(1, 30) = 3.30$, $p \leq .079$, $\eta^2_p = .099$. The difference between randomization block RTs and baseline block RTs was significantly higher in session 3 than in sessions 1 and 2, both $t(31) > 2.18$, both $p \leq .05$, between which the randomization costs did not differ significantly, $t(31) = 0.57$. This pattern reflects that the amount of acquired sequence knowledge increased with practice.

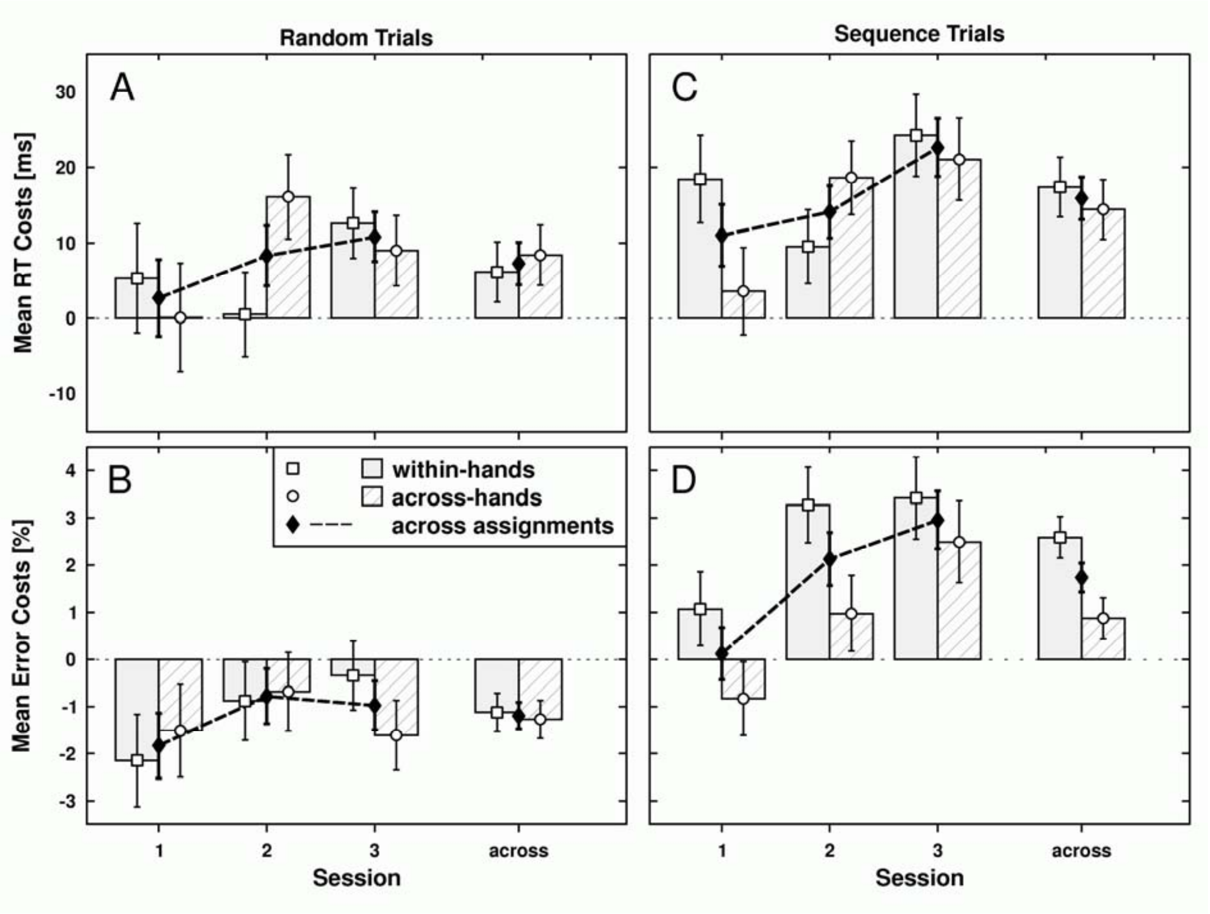


Figure 16. Mean RT and error costs in randomization test blocks separately for the random trials (left panels) and for sequence trials (right panels), separately for as well as across the two assignments, and separately for each session as well as across all sessions in Experiment 5. Error bars represent standard errors of the means.

Randomization Probes: Sequence-trial PEs. The Session × Blocktype × Assignment ANOVA on sequence trial PEs revealed a significant main effect Blocktype, $F(1, 30) = 31.49$, $p \leq .001$, $\eta_p^2 = .512$, which was further qualified in a Blocktype × Session interaction, $F(2, 60) = 5.94$, $p \leq .01$, $\eta_p^2 = .165$, and a Blocktype × Assignment interaction, $F(1, 30) = 7.65$, $p \leq .01$, $\eta_p^2 = .203$. Among the other main effects and interactions the Assignment factor came closest to reaching significance but did not, $F(1, 30) = 2.40$, $p \leq .132$, $\eta_p^2 = .074$; all other $F < 0.63$.

The Blocktype × Session interaction reflected that PEs were significantly higher in randomization blocks than in baseline blocks in sessions 2 and 3, both $F(1, 30) > 14.15$, $p \leq .001$, $\eta_p^2 > .320$, but not in session 1, $F(1, 30) = 0.05$, $\eta_p^2 = .002$. Specifically, PE randomization costs were significantly higher in sessions 2 and 3 than in session 1, both $t(31) > 2.39$, both $p \leq .05$, but they did not differ significantly between sessions 2 and 3, $t(31) = 0.99$.

The Blocktype × Assignment interaction reflected that the increase of PEs in randomization blocks relative to baseline blocks was more pronounced under the within-hands assignment, $F(1, 15) = 30.12$, $p \leq .001$, $\eta_p^2 = .668$, than under the across-hands assignment, $F(1, 15) = 4.85$, $p \leq .05$, $\eta_p^2 = .244$, indicating that sequence learning was more pronounced under the former than under the latter assignment (see Figure 16D).

Table 6
Results of the Session (1, 2, 3) × Blocktype (baseline vs.randomization block) × Assignment (within-hands vs. across-hands) ANOVA on reaction time (RT) data from sequence trials in Experiment 5.

	ANOVA on sequence trial RTs					
	df1	df2	*F*	*p*		η_p^2
Assignment	1	30	0.17	.681		.006
Session	2	60	228.869	.000	***	.884
Blocktype	2	30	32.369	.000	***	.519
S × A	2	60	2.945	.060	+	.089
B × A	1	30	0.280	.601		.009
S × B	2	60	3.664	.032	*	.109
S × B × A	2	60	3.628	.033	*	.108

Note. Significance levels are coded as follows: $^+$ indicates $p \leq .10$, * indicates $p \leq .05$, ** indicates $p \leq .005$, and *** indicates $p \leq .001$.

Continuous Measure of Sequence Learning: RTs. Apart from being evident in randomization test blocks, sequence learning could have also expressed itself in regular blocks in better performance on sequence trials than on random trials. For the analysis of this continuous measure of sequence learning, data from the 21 regular blocks of each session were aggregated into 10 epochs with the first epoch in each session encompassing blocks 1–3 and all subsequent epochs encompassing two blocks (i.e., 4+5, 6+7, ... 18+19, 20+22). A Session × Epoch × Trialtype × Assignment ANOVA on median RTs revealed several significant main effects and interactions (see Table 7) including the three-way Session × Epoch × Assignment interaction. In order to unpack this interaction, separate Epoch × Trialtype × Assignment ANOVAs were computed for each session.

Table 7

Results of the Session (1, 2, 3) × Epoch (1–10) × Trialtype (sequence vs. random trials) × Assignment (within-hands vs. across-hands) ANOVA on reaction time (RT) data from regular blocks in Experiment 5.

	ANOVA on RTs					
	df1	df2	ε_{GG}	F	p	η_p^2
Session	2	60	.550***	357.58	.000 ***	.923
Epoch	9	270	.237***	101.59	.000 ***	.772
Trialtype	1	30		8.04	.008 **	.211
Assignment	1	30		0.30	.864	.001
S × A	2	60		4.64	.013 *	.134
E × A	9	270		5.08	.000 ***	.145
T × A	1	30		0.31	.581	.010
S × E	18	540	.187***	71.71	.000 ***	.705
S × E × A	18	540		6.11	.000 ***	.169
S × T	2	60	.613***	9.74	.002 **	.245
S × T × A	2	60		2.94	.060 +	.089
E × T	9	270	.451***	1.46	.218	.046
E × T × A	9	270		1.70	.089	.054
S × E × T	18	540	.323***	1.24	.223	.040
S × E × T × A	18	540		0.70	.816	.023

Note. Significance levels are coded as follows: + indicates $p \le .10$, * indicates $p \le .05$, ** indicates $p \le .01$, and *** indicates $p \le .001$.

For session 1, there was a significant main effect Epoch, $F(9, 270) = 103.96$, $p \le .001$, $\eta_p^2 = .776$, $\varepsilon_{GG} = .246$, as well as a significant interaction between the factors Epoch and Assignment, $F(9, 270) = 7.14$, $p \le .001$, $\eta_p^2 = .192$, $\varepsilon_{GG} = .357$. The interaction reflected that from an initially slower RT level in the within-hands than in the across-hands condition, response speed increased more steeply in the former than in latter condition so that from the 6th epoch onwards RTs did not differ between the two conditions (see Figure 15). No other main effects or interactions were significant, all $F < 1.07$, all $\eta_p^2 < .035$. Notably, RTs on sequence trials did not differ significantly from those on random trials, neither in the within-hands nor in the across-hands condition.

For session 2, the main effects Epoch and Trialtype as well as their interaction were significant, all $F > 3.42$, all $p \le .01$, all $\eta_p^2 > .102$. The interaction reflected that sequence learning as indicated by significantly faster responding on sequence than on random trials emerged across epochs and was evident only in the second half of session 2. No other main effects or interactions were significant, all $F < 1.02$, all $\eta_p^2 < .033$. In particular, sequence learning did not differ significantly between the two assignments.

Analysis of data from session 3 yielded significant main effects Epoch and Trialtype, both $F > 7.92$, both $p \leq .001$, both $\eta_p^2 > .208$, indicating (a) an overall decline of RTs across epochs and (b) generally faster RTs on sequence than on random trials. The benefit of sequence relative to random trials was numerically but not significantly higher under the within-hands assignment than under the across-hands assignment, $F(1, 30) = 1.76$, $\eta_p^2 = .055$. No other main effects or interactions were significant, all $F < 1.03$, all $\eta_p^2 < .034$.

Table 8

Results of the Session (1, 2, 3) × Epoch (1–10) × Trialtype (sequence vs. random trials) × Assignment (within-hands vs. across-hands) ANOVA on percent error (PE) data from regular blocks in Experiment 5.

	ANOVA on PEs						
	df1	df2	ε_{GG}	F	p		η_p^2
Session	2	60	.702***	7.18	.005	**	.193
Epoch	9	270	.552***	1.64	.154		.052
Trialtype	1	30		5.15	.031	*	.146
Assignment	1	30		0.23	.634		.008
S × A	2	60		0.06	.887		.002
E × A	9	270		1.41	.226		.045
T × A	1	30		0.45	.507		.015
S × E	18	540	.455***	7.42	.000	***	.198
S × E × A	18	540		0.95	.477		.031
S × T	2	60	.849 +	9.31	.000	***	.237
S × T × A	2	60		0.10	.906		.0003
E × T	9	270	.784	1.18	.309		.038
E × T × A	9	270		1.05	.402		.034
S × E × T	18	540	.584	0.98	.487		.031
S × E × T × A	18	540		1.00	.460		.032

Note. Significance levels are coded as follows: + indicates $p \leq .10$, * indicates $p \leq .05$, ** indicates $p \leq .01$, and *** indicates $p \leq .001$.

Continuous Measure of Sequence Learning: PEs. An analogous Session × Epoch × Trialtype × Assignment ANOVA on PEs revealed several significant main effects and interactions (see Table 8). Separate Epoch × Trialtype × Assignment ANOVAs for each session revealed main effects Epoch in all sessions, all $F(9, 270) > 3.03$, all $p \leq .01$, all $\eta_p^2 > .091$. In sessions 2 and 3, PEs were significantly lower on sequence than on random trials, both $F(1, 30) > 8.40$, both $p \leq .01$, both $\eta_p^2 > .218$. This was not the case in session 1, $F(1, 30) = 0.08$, $\eta_p^2 = .002$. For session 2, the Epoch × Trialtype × Assignment interaction approached but did not reach significance, $F(9, 270) = 1.90$, $p \leq .086$, $\eta_p^2 = .060$, $\varepsilon_{GG} = .646$. No other main effects or interactions were significant, all $F < 1.65$, all $\eta_p^2 < .052$.

To summarize (see Figure 17), sequence learning as reflected in faster responding and lower error rates on sequence than on random trials in regular blocks emerged with practice over the course of the experiment. In RTs, the difference between random and sequence trials was numerically but not significantly larger under the within-hands than under the across-hands assignment.

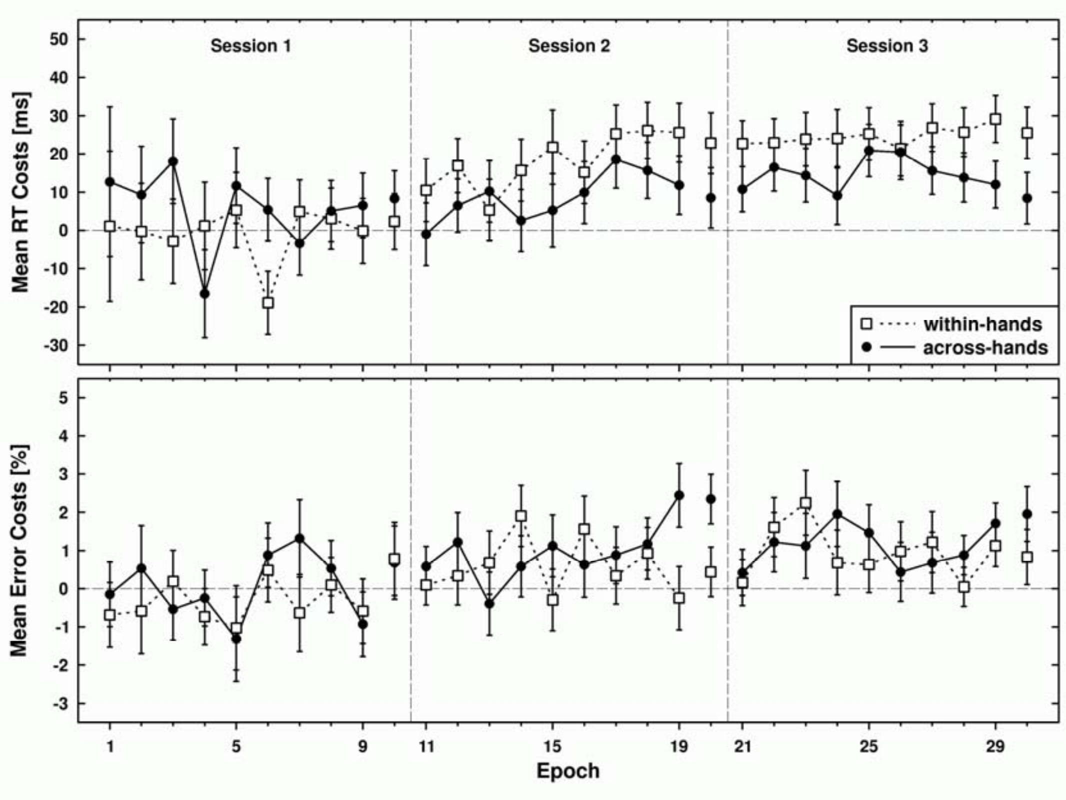


Figure 17. Mean differences in RTs and error rates between sequence trials and random trials in regular blocks (aggregated into epochs) across sessions of Experiment 5 separately for the two assignments. Error bars represent standard errors of the means. Note: Epochs 1, 11, and 21 encompass 3 blocks, all other epochs encompass 2 blocks. Epochs 10, 20, and 30 are the regular blocks in which the randomization test blocks were embedded.

Generation Task. Participants' performance in the generation task was scored separately for the inclusion and the exclusion condition by determining for each of the 62 triples contained in the 64-trial sequence generated by participants whether it was a triple that also occurred in the (to-be-recalled or to-be-avoided) practiced sequence or not. Perfect recall of the sequence under inclusion instructions yields the maximum score of 62 corresponding triples, and perfect avoidance of second-order transitions from the practiced sequence under exclusion instructions yields the minimum score of 0 corresponding triples. The acquisition of explicit sequence knowledge would be indicated by better recall performance under inclusion than under exclusion instructions (cf. Destrebecqz and Cleeremans, 2001; see also Jacoby, 1991).

The number of corresponding triples was analyzed in a 2 (task: inclusion vs. exclusion) × 2 (assignment: within-hands vs. across-hands) mixed-factors ANOVA with repeated measures on the first factor. Relevant means are given in Table 9. Overall, recall performance was rather poor, and neither participants in the within-hands nor participants in the across-hands condition appear to have acquired substantial explicit knowledge about the implemented sequence. Numerically, participants generated more corresponding triples under inclusion instructions than under exclusion instructions, but this difference was not statistically significant, $F(1, 30) = 2.74$, $p \leq .108$, $\eta_p^2 = .084$. Similarly, the tendency of participants in the within-hands assignment condition to generate more corresponding triples than participants in the across-hands assignment condition approached but did not reach statistical significance, $F(1, 30) = 3.70$, $p \leq .064$, $\eta_p^2 = .110$. Importantly, this tendency was not significantly restricted

Table 9
Mean number of corresponding triples (standard error of the mean in parentheses) produced in the post-experimental sequence generation task in Experiment 5 separately for as well as across the instruction conditions and the assignments conditions.

	Instructions		
	inclusion	exclusion	mean
Assignment			
within-hands	16.6 (1.32)	15.4 (1.32)	16.0 (0.98)
across-hand	14.6 (1.16)	12.1 (1.14)	13.3 (0.98)
mean	15.6 (0.88)	13.8 (0.87)	

to the condition under inclusion instructions as suggested by the non-significant Task × Assignment interaction, $F(1, 30) = 0.37$, $\eta_p^2 = .012$. The difference between corresponding triples recalled under inclusion and exclusion conditions did not differ significantly between the across-hands condition ($M = 2.44$; $SE = 1.47$) and the within-hands condition ($M = 1.13$; $SE = 1.58$), $t(30) = 0.61$.

4.3.3 Discussion

On each trial in Experiment 5, a stimulus appeared in one of eight locations and participants had to press the corresponding key. The stimuli appearing in four of these locations were part of a repeating structured sequence, whereas the stimuli appearing in the remaining four locations were randomly selected. Sequence stimuli (sequence trials) appeared alternately with random stimuli (random trials). The assignment of stimulus locations to fingers of the left and the right hand was either such that participants responded with fingers of one hand to all sequence stimuli and with fingers of the other hand to all random stimuli (within-hands assignments) or such that participants responded with two fingers of the left and two fingers of the right hand to the sequence stimuli and with the remaining fingers to random stimuli (across-hands assignment). Sequence learning was assessed at the end of each of three sessions by replacing sequence stimuli with random stimuli.

Participants exhibited clear signs of learning the sequence, which was regularly interrupted by random trials: On sequence trials, randomization of the sequence in test blocks led to performance decrements relative to baseline blocks. In contrast, on random trials, test block decrements in response speed were accompanied by benefits in response accuracy indicating a speed accuracy trade-off. Thus, indications of sequence learning were restricted to sequence trials indicating that participants did not learn a compound probabilistic sequence comprising both sequence and random trials. Although not the primary concern addressed with Experiment 5, it cannot be stressed enough how remarkable it is that sequence learning occurs at all under the implemented conditions, which effectively require participants to learn about regular transitions spanning 5 trials as every triple of the second-order conditional sequence is interrupted by two interleaved random trials.

The focus of Experiment 5 was on possible differences in sequence learning between the within-hands and the across-hands assignment of the sequence. Indeed, a benefit associated with practicing the sequence with fingers of one hand compared to practicing it with fingers of both hands (i.e., more pronounced sequence learning under the within-hands than under the across-hands assignment) was evident in error data. Although this advantage of the within-hands assignment was not statistically significant in RT data, there were no significant indications that it might have been due to participants in the within-hands condition trading off speed and accuracy differently than participants in the across-hands condition. The within-hands advantage is consistent with the operation of separate learning modules for the two hands. Although no test for transfer was implemented with which it could have been determined whether acquired sequence knowledge was effector-specific, the within-hands advantage is also in line with the notion that effector-specific sequence learning occurs in terms of the development of coarticulatory optimization which has been argued to be particularly important for sequence learning with fingers of one hand as compared to sequence learning with fingers of both hands (Verwey & Clegg, 2005). Importantly, the advantage observed for the within-hands assignment cannot be attributed to the acquisition of more explicit sequence learning in the within-hands than in the across-hands condition. Participants appeared to have not acquired substantial explicit knowledge about the implemented sequence in the first place. This conclusion is in line with results reported by D. V. Howard et al. (2004) as well as J. H. Howard et al. (2004) who also found that sequence learning in a similar alternating SRT task was largely implicit (see also Negash, Howard, Japikse, & Howard, 2003).

These conclusions are limited by the fact that a comparable within-hands advantage was not significant when looking at the continuous measure of sequence learning available when comparing sequence-trial RTs with random-trial RTs within regular blocks, although the data are suggestive of such a difference. However, it can be argued that randomizing stimuli in those very same locations in which stimuli were structured during acquisition (thus randomizing responses [a] on those keys on which and [b] with those fingers with which responding was structured during acquisition) constitutes a more immediate test of sequence learning than comparing learning of a repeating sequence implemented for one half of stimulus locations, keys, and fingers with non-learning of a random sequence implemented for the other half of stimulus locations, keys, and fingers. In other words, the continuous learning measure might be less sensitive than the randomization test. Therefore, the results obtained with the latter might deserve to be given more weight than the results obtained with the former.

To summarize, Experiment 5 provided evidence suggesting an advantage for learning a sequence when responding with fingers of one hand compared to learning the same sequence when responding with fingers of both hands. This in turn is consistent with the idea that a separate learning module for each hand might exist.

5 Experiments 6 & 7: Unimanual SRT Task

The results of the experiments presented so far demonstrate that independent learning of extensively practiced hand-related sequences persists even when the basis for separate perceptual learning of the two sequences is eliminated (as in single-stimulus condition of Experiment 2 and in Experiments 3–4), thus, implicating that the obtained independent learning is motor based. This conclusion is underpinned by the associated lack of evidence for intermanual transfer (in the single-stimulus condition of Experiment 2 as well as in Experiments 3 and 4). Together with the results from Experiment 5, which suggest that sequential responding with fingers of one hand results in more pronounced sequence learning than sequential responding with fingers of both hands, these findings point to the existence of a separate sequence learning module for each hand, the operation of which appears to result in the acquisition of hand-specific sequence knowledge, which is not available for intermanual transfer. However, the experiments reported so far have not investigated the possibility that sequence knowledge might transfer from one hand to homologous fingers of the other hand (cf. Deroost et al., 2006; Wachs et al., 1994). This issue was addressed in Experiment 6.

5.1 Experiment 6

The conflicting findings regarding the intermanual transfer of sequence knowledge between homologous fingers have been reviewed in the Introduction. The present experiment was designed to improve on previous studies which have used horizontally aligned stimulus locations and response keys (e.g., Deroost et al., 2006; Grafton et al., 2002). This regular horizontal setup is afflicted with the difficulty that assessing performance of the sequence of homologous finger movements with the unpracticed hand requires mirroring the sequence of imperative stimuli presented during training with the practiced hand so that the sequence in which response keys are to be pressed was also mirrored. In such a setting, intermanual transfer is indicated by better performance for the mirrored sequence than for a random or an unpracticed sequence (e.g., Deroost et al., 2006; Grafton et al., 2002). However, there are reasons to doubt that such a mirror sequence benefit truly reflects transfer to homologous fingers of the unpracticed (contralateral) hand: A mirror sequence benefit has also been observed for the practiced (ipsilateral) hand (Verwey & Clegg, 2005), which suggests that the mirror sequence benefit might rely on a more abstract level of sequence representation than the purported sequence representation in terms of finger movements equally applicable to homologous fingers of either hand. This problem was avoided here by vertically aligning the response keys so that for both the practiced hand and the transfer hand executing the structured sequence involved (a) pressing the same sequence of identical response keys (b) with the same sequence of movements of homologous fingers in response to (c) the same sequence of identical imperative stimuli. Thus, the finding of imperfect intermanual transfer under these conditions could only be ascribed to truly effector-specific sequence knowledge. In that sense, Experiment 6 constituted a maximally conservative test of effector-specific sequence knowledge by creating optimal conditions for intermanual transfer as all sequence knowledge pertaining to the sequence of stimuli, response locations, or homologous effectors should be easily transferable to the other hand under these conditions. Furthermore, Experiment 6 was designed to obtain a fine-grained record of the development of effector-specific sequence knowledge with increasing practice across several sessions.

5.1.1 Method

Participants. Sixteen volunteers (mean age 20.4 years) participated in partial fulfillment of course requirements. Only participants who reported to be right-handed were recruited.

Task and Design. Participants responded to the position of a stimulus by pressing the compatibly assigned key. Stimulus positions as well as keys were vertically aligned (see Figure 18). Responses were to be executed in blockwise alternation either with the left or with the right hand.

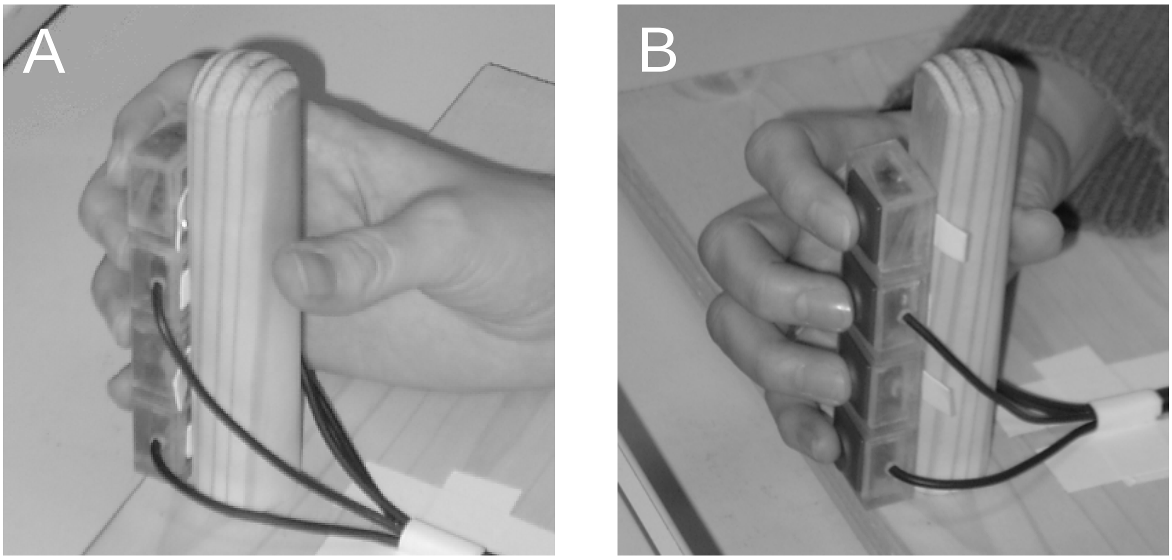


Figure 18. Photographs of the *key rod* response device used in Experiment 6: Response keys were vertically aligned on a wooden stick which was attached perpendicular to the table top. Photograph (A) highlights the grip-like hand position assumed by participants during operation of the keys. Photograph (B) highlights the assignment of fingers to keys.

The imperative stimuli appeared in a repeating structured sequence when participants responded with one hand (henceforth, structure hand) but randomly when they responded with the other hand (henceforth, random hand). The assignment of the dominant and the non-dominant hand as either the structure or the random hand was counterbalanced across participants.

The vertical setup ensured not only comfortable operation of keys with either hand but also that participants used homologous fingers for pressing the same key with either hand (e.g., the top key is pressed with the index finger of either hand). Responding with the left and the right hand in blockwise alternation ensured that participants practiced the stimulus-response mappings equally with both hands.

The critical manipulations were (a) randomizing the structured sequence and (b) transferring the structured sequence to the random hand. Sequence learning would express itself in faster responding to the structured sequence than to random sequences. To the extent that this structure benefit is observed not only for the structure hand but also for the random hand (i.e., in transfer blocks), the acquired sequence knowledge is available for intermanual transfer and thus effector-independent. Any non-transferable, effector-specific sequence knowledge is implicated to the extent that responding to the structured sequence is faster with the structure hand than with the random hand (i.e., in transfer blocks).

Because effector-specific sequence knowledge might develop quite slowly and only as a result of extensive practice, randomization and transfer test blocks were repeated at the end of each of 5 sessions in order to investigate the time-course of effector-specific sequence learning. Additional test blocks were implemented in which unpracticed structured sequences appeared for the random hand. This control condition was introduced in order to assess the possibility of sequence learning with the random hand within a single block.

Apparatus and Materials. Stimulus presentation and response registration was controlled by the E-Prime software package (Schneider et al., 2002). Four response keys were mounted vertically on a rod attached perpendicular to the table top, on that side of the rod facing away from participants (see Figure 18). The distance between the centers of adjacent keys was 2.5 cm. The keys were connected to the computer via the parallel port.

Stimuli were presented on a 17-inch computer monitor. An asterisk appeared in black on a white background in any one of four vertically aligned locations on the screen each marked by a square also appearing in black (side length 22 mm). There was an equal distance of 6 mm between any two adjacent squares. The keys were assigned compatibly to the squares (locations) on the screen. The keys in turn were assigned from top to bottom to the index, middle, ring, and little finger of either hand.

A 12-element second-order conditional sequence (ABACDBCADCBD) was used as the primary structured sequence. Four additional second-order conditional sequences which shared not a single 3-tuple with the primary structured sequence served as structured sequences in the control condition (ABCBADBDCDAC, ABCDACBADBDC, ABDBADACBCDC, ABDCACBCDADB).

The random sequences presented in random-hand blocks were constructed so that within each block (a) each location appeared equally often, (b) a maximum of 4 3-tuples appeared which are also included in the primary structured sequence, and (c) each of the remaining 3-tuples appeared between 3 and 6 times. The random sequences presented in randomization test blocks adhered to the same constraints but were shorter as randomization entailed embedding 96 random trials in 48 structured trials (24 before and 24 after randomization).

The elements (i.e., A, B, C, D) in the stimulus sequences were assigned to the four stimulus locations on the screen (i.e., 1, 2, 3, 4 from top to bottom) according to a Latin square scheme. Note that this does not alter the statistical properties (e.g., location frequencies, transition probabilities) of any of the sequences. The four implemented assignments were counterbalanced across participants.

Procedure. The experiment was conducted in five sessions scheduled for consecutive days. Each session contained 30 blocks, 15 blocks with the sequence hand alternating with 15 blocks with the random hand. Whether a session started with a sequence-hand block or a random-hand block was randomly determined for each participant. As an exception, in Session 1 the first block in which participants performed with the sequence hand served as a warm-up block during which stimuli were presented in a random sequence.

Three of the 30 blocks in each session were test blocks (randomization [R], transfer [T], control condition [C]). Randomization test blocks always occurred either before or after the other two types of test blocks. For each participant, this ordering of test blocks alternated between sessions (R first vs. R last), with one half of participants beginning with the one ordering, and the other half of the sample beginning with the other ordering. Independently of this counterbalancing of the position of randomization blocks relative to the other test blocks, the ordering of the transfer and control condition blocks alternated between sessions (TC vs. CT), with one half of participants beginning with the one ordering, and the other half of the sample beginning with the other ordering. Together, these counterbalancing measures resulted in 4 possible test block schedules which were counterbalanced across participants.

Specifically, the randomization test block was either the 10th or the 14th sequence-hand block (i.e., the 19th or 27th overall block in the session, if the session began with a sequence-hand block, or the 20th or 28th overall block in the session, if the session began with a random-hand block). Accordingly, the transfer and control condition blocks were either the 12th and 14th or the 10th and 12th random-hand block, respectively (i.e., the 20th, 24th, or 28th overall block or the 19th, 23rd, or 27th overall block; see Figure 19 for an exemplary illustration). Thus, on average, participants completed 120, 288, 456, 624, and 792 sequence repetitions prior to the randomization block in session 1, 2, 3, 4, and 5, respectively (not counting sequence repetitions in transfer blocks and at the start and the end of randomization blocks). Control condition structured sequences were randomly assigned to the five sessions with one of them appearing in two sessions.

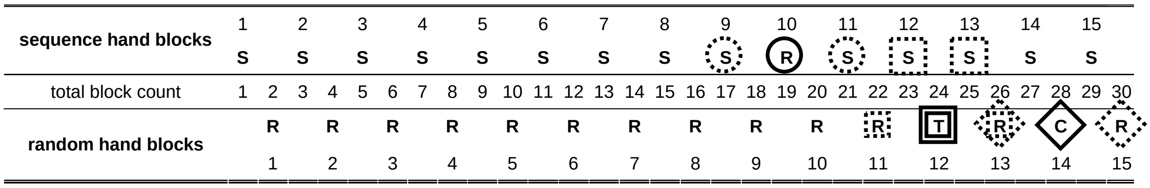


Figure 19. Example of a possible test block schedule in Experiment 6. Each type of test block is represented by a different shape drawn with a solid line (circle = randomization test block [R]; square = transfer test block [T]; diamond = control condition test block with unpracticed structured sequence [C]). Blocks serving as baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. *Note.* S/T = practiced structured sequence block; R = random sequence block; C = unpracticed structured sequence.

Each block comprised 144 trials. Each sequence-hand block began at a randomly determined position in the 12-element sequence. Each trial began with the presentation of the imperative stimulus. Following the participant's response, 120 ms elapsed before the next trial was initiated. In case of an error, the German word for error (“Fehler!”) appeared in red color centered below the vertical row of squares and accompanied by a short beep tone for the duration of this response-stimulus interval.

Written instructions were presented on the screen at the beginning of session 1, informing participants about the assignment of locations on the screen to keys and to fingers as described above. Participants were told that on every trial an asterisk would appear in one of the locations, indicating which key to press. Participants were also told that they would be responding in blockwise alternation with the left and the right hand, and they were asked to rest the fingers of the respective hand lightly on the keys. Both speed and accuracy were stressed in the instructions. Specifically, participants were asked to try and keep the number of errors per block below 10. No mention was made of regularities in the order of stimuli. These instructions were repeated before each of the following sessions. Prior to each block, additional written instructions informed participants which hand to use in the upcoming block. Participants initiated each block by pressing the space bar on the keyboard with the other hand. After completion of each block, a text on the screen provided participants with feedback about their mean RT as well as the number of errors in the previous blocks and reminded them of the requirements regarding speed and accuracy. This feedback text was presented for 20 seconds. The experimenter was present in the laboratory throughout the experiment in order to verify that participants did indeed switch hands as instructed.

After completing session 5, participants were debriefed about the presence of a sequence for one of the hands and its exact length, and they were asked to recall that sequence. Specifically, participants were to write down the sequence of stimuli or the sequence of key presses, and they were encouraged to guess if they could not recall parts of the sequence. Participants were also told that they could use their hand during recall and start at any position in the sequence.

5.1.2 Results

In order to ensure a maximally sensitive test for completeness of intermanual transfer, statistical analyses were restricted to data from the second half of each block. In this way, analyses were biased in favor of complete intermanual transfer for the following reasons: By the second half of transfer blocks (a) participants had ample time to notice the presence of the structured sequence instead of a random sequence, and (b) some within-block learning of the structured sequence might have occurred for the random hand.

RTs from error trials (4.1%) were excluded from analyses as were RTs more than 3 SD above or below the z-transformed mean RT as determined separately for each participant and each block within each session (0.8%). Median RTs and error rates (percent errors; PEs) were computed for each type of test block and the corresponding baseline blocks separately for each session (see Figure 20). The baseline for random trials in randomization blocks consisted of adjacent structure-hand blocks. Similarly, the baselines for transfer and control condition blocks consisted of adjacent random-hand blocks. Random-hand performance in transfer blocks was also compared with structure-hand performance in adjacent structure-hand blocks in order to assess completeness of intermanual transfer (cf. Figure 19). Unlike previous experiments, results are not presented in terms of RT/PE costs in order to give readers a more immediate sense of the development of absolute levels of RT and PE in the different conditions across the experiment.

Unless otherwise noted RT and PE data were analyzed in Session (1, 2, 3, 4, 5) × Blocktype repeated-measures analyses of variance (ANOVA). Depending on the test block to be analyzed, median RTs and PEs from that test block and from the corresponding baseline blocks were assigned to the two levels of the Blocktype factor. Direction of transfer (from the dominant to the non-dominant hand vs. from the non-dominant to the dominant hand) did not yield a significant main effect and was not involved in any significant interactions when included as a factor in any of the ANOVAs reported below.[4] Therefore and in order to focus presentation of results, this factor was dropped from all analyses. All pairwise comparisons are two-tailed. As in previous experiments, the Greenhouse-Geisser correction was applied in repeated-measures analyses of variance whenever necessary.

Randomization Blocks. Structure-hand RTs were significantly slower on random trials than on structured baseline trials, thus indicating sequence learning in each session, all $t(15) > 8.41$, all $p \le .001$, as well as across sessions, $F(1, 15) = 310.00$, $p \le .001$, $\eta_p^2 = .954$. Sequence learning increased across sessions as indicated by the significant Session × Blocktype interaction, $F(4, 60) = 49.87$, $p \le .001$, $\eta_p^2 = .769$, $\varepsilon_{GG} = .651$. The main effect Session was also significant, $F(4, 60) = 142.25$, $p \le .001$, $\eta_p^2 = .905$, $\varepsilon_{GG} = .467$, reflecting a general decrease in response latencies across sessions.

Structure-hand PEs were also numerically higher on random trials ($M = 4.4\%$, $SE = 0.4$) than on structured baseline trials ($M = 3.3\%$, $SE = 0.5$) but the main effect Blocktype was not significant, $F(1, 15) = 3.25$, $p \le .092$, $\eta_p^2 = .178$. The main effect Session and the Session × Blocktype interaction were not significant either, both $F(4, 60) < 1.87$, both $\eta_p^2 < .111$.

Transfer Blocks. Random-hand RTs were faster on transferred structured sequence trials than on random baseline trials, thus indicating intermanual transfer in each session, all $t(15) > 9.08$, all $p \le .001$, as well as across sessions, $F(1, 15) = 178.88$, $p \le .001$, $\eta_p^2 = .923$. The significant main effect Session, $F(4, 60) = 126.71$, $p \le .001$, $\eta_p^2 = .894$, $\varepsilon_{GG} = .584$, reflected a general decrease in response latencies across sessions. The significant Blocktype × Session

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[4] Only one interaction (Session × Direction of Transfer) in one of the analyses (Session × Blocktype [unpracticed structured vs. random] × Direction of Transfer ANOVA on PEs) came close to but did not reach significance, $F(4, 56) = 2.47$, $p \le .095$, $\eta_p^2 = .150$, $\varepsilon_{GG} = .563$. This interaction hinted at PEs in control condition blocks and corresponding baseline blocks decreasing over sessions in the dominant-to-non-dominant transfer group, while an increase over sessions appeared to be present in the non-dominant-to-dominant group. All other $F < 1.49$, all other $\eta_p^2 < .096$.

interaction, $F(4, 60) = 34.52$, $p \leq .001$, $\eta_p^2 = .697$, indicated that intermanual transfer increased across sessions.

Random-hand PEs were also numerically higher on random trials ($M = 4.9\%$, $SE = 0.4$) than on structured baseline trials ($M = 4.0\%$, $SE = 0.5$) but the main effect Blocktype was not significant, $F(1, 15) = 3.88$, $p \leq .068$, $\eta_p^2 = .205$. The main effect Session and the Session × Blocktype interaction were not significant either, both $F(4, 60) < 1.50$, both $\eta_p^2 < .091$.

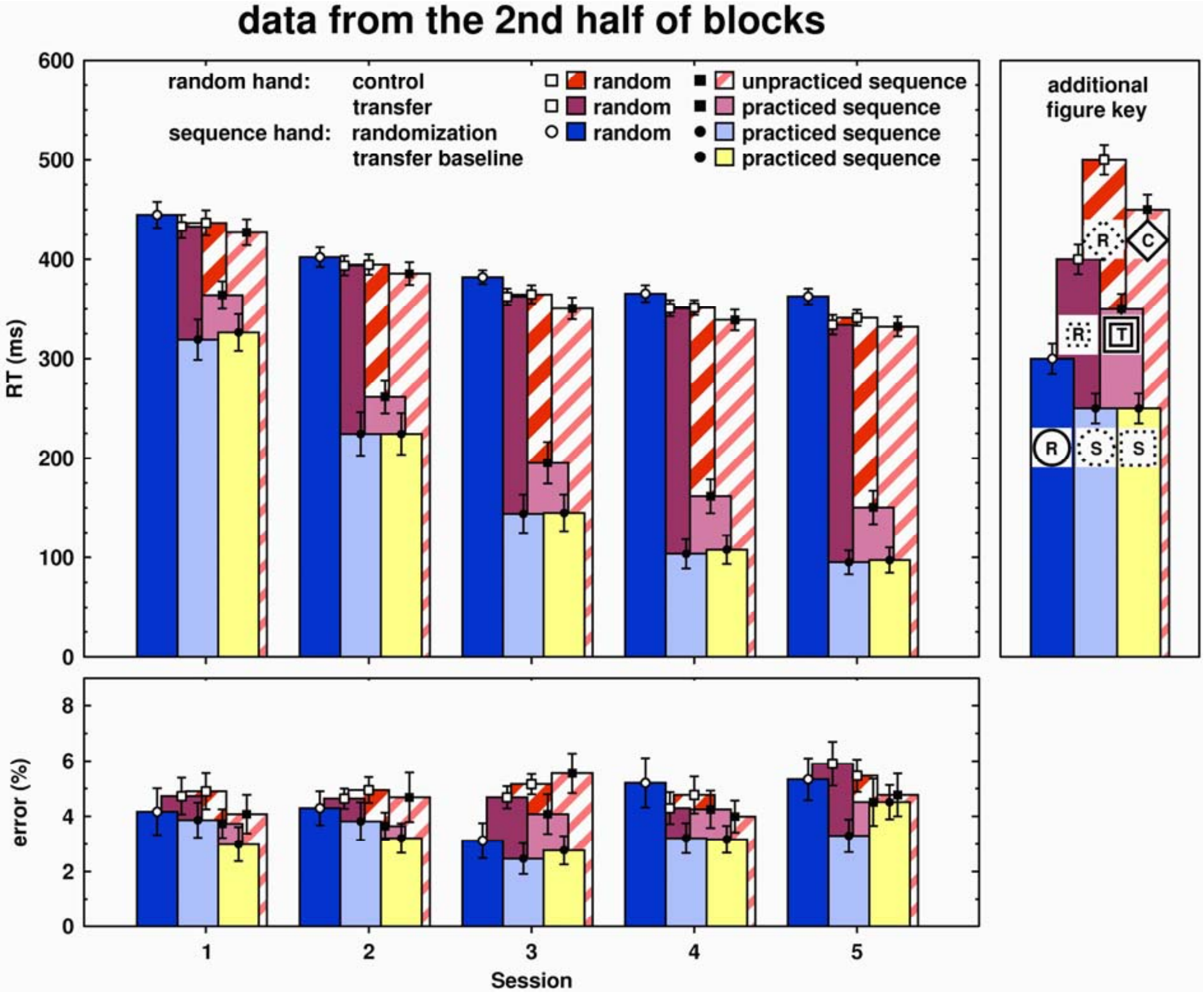


Figure 20. Means of individual median RTs and error rates in the various types of test and baseline blocks separately for the five sessions in Experiment 6. Only data from the second half of blocks were included. Error bars represent standard errors of the means. *Note*. For the additional figure key (cf. Figure 19), each type of test block is represented by a different shape drawn with a solid line (circle = randomization test block [R]; square = transfer test block [T]; diamond = control condition test block with unpracticed structured sequence [C]). Blocks serving as baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. S/T = practiced structured sequence block; R = random sequence block; C = unpracticed structured sequence.

The observed benefit for responding with the random hand to the practiced structured sequence as compared to random sequences was not due to within-block learning. Although responding was significantly faster in control condition blocks, in which an unpracticed structured sequence was presented (*M* = 366.9 ms, *SE* = 10.2), than in random baseline blocks (*M* = 377.6 ms, *SE* = 8.9), $F(1, 15) = 15.27$, $p \leq .001$, $\eta_p^2 = .505$, this structured sequence benefit, which reflects within-block learning, amounted only to 10.7 ms. The observed intermanual transfer was much larger than that (the mean structured sequence benefit for the practiced sequence increased across sessions from 69.3 ms in session 1 to 132.0 ms in session 2, 166.8 ms in session 3, 188.8 ms in session 4, and 183.6 ms in session 5) and thus cannot be completely accounted for by within-block learning. The main effect Session was also significant, $F(4, 60) = 88.54$, $p \leq .001$, $\eta_p^2 = .855$, $\varepsilon_{GG} = .503$, but the interaction was not significant, $F(4, 60) = 0.26$, $\eta_p^2 = .017$, $\varepsilon_{GG} = .725$. An analogous ANOVA on PEs revealed no significant effects, all $F < 2.05$, all $\eta_p^2 < .032$.

Completeness of Intermanual Transfer. Despite considerable intermanual transfer, responding to the practiced structured sequence was still significantly slower with the random hand than with the sequence hand in each session, all $t(15) > 3.54$, all $p \leq .005$. In a Session × Hand (sequence hand vs. random hand) repeated-measures ANOVA, this expressed itself as a significant main effect Hand, $F(1, 15) = 66.58$, $p \leq .001$. $\eta_p^2 = .816$. Also, the main effect Session was significant, $F(4, 60) = 149.08$, $p \leq .001$, $\eta_p^2 = .909$, $\varepsilon_{GG} = .597$, reflecting generally decreasing RTs over the course of the experiment. The Session × Hand interaction was not significant, $F(4, 60) = 0.89$, $\eta_p^2 = .056$, $\varepsilon_{GG} = .595$. An analogous ANOVA on PEs also yielded a significant main effect Hand, $F(1, 15) = 5.85$, $p \leq .05$, $\eta_p^2 = .281$, indicating that responding to the practiced structured sequence was more erroneous with the random hand (*M* = 4.0%, *SE* = 0.5) than with the sequence hand (*M* = 3.3%, *SE* = 0.4) although none of the pairwise comparisons computed separately for each session were significant, all $t(7) < 1.81$, all $p > .090$. Neither the main effect Session nor the Session × Hand were significant, both $F(4, 60) < 1.59$, both $\eta_p^2 < .096$.

One might be concerned that comparing performance between hands is possibly contaminated by general differences between the dominant and the non-dominant hand in terms of performance efficiency, which are unrelated to the acquisition and intermanual transfer of sequence knowledge. However, any such contaminating influences should be equally distributed across transfer and baseline conditions in the experimental design as direction of transfer (dominant to non-dominant vs. non-dominant to dominant) was counterbalanced across participants. Also, direction of transfer did not yield any significant main effects or interactions in any of the analyses as noted above. Yet, the lack of a significant effect must always be interpreted cautiously. Therefore, this concern was addressed in additional analyses.

First, the analyses for incompleteness of intermanual transfer were repeated as just described but restricted to data from that sub-sample of participants for whom the structured sequence was transferred from the non-dominant to the dominant hand. Despite the reduction in statistical power associated with the smaller sample size (n=8), results largely confirmed those from the analysis for the entire sample. Responding to the practiced structured sequence was slower with the random-hand than with the sequence-hand in each session. This difference failed significance in session 1, $t(7) = 1.73$, $p \leq .126$, but was significant in sessions 2–5, all $t(7) > 2.68$, all $p \leq .05$. Accordingly, the Session × Hand ANOVA showed a significant main effect Hand, $F(1, 7) = 34.44$, $p \leq .001$. $\eta_p^2 = .831$, which was not significantly moderated by Session, $F(4, 28) = 0.79$, $\eta_p^2 = .101$. The significant main effect Session, $F(4, 28) = 55.02$, $p \leq .001$, $\eta_p^2 = .887$, reflected generally decreasing RTs over the course of the experiment. An analogous ANOVA on PEs also yielded a significant main effect Hand, $F(1, 7) = 7.17$, $p \leq .05$, $\eta_p^2 = .506$, indicating that responding to the practiced structured sequence was more erroneous with the random hand (*M* = 4.2%, *SE* = 0.6) than with the sequence hand (*M* = 3.2%, *SE* = 0.5), although separate pairwise comparisons were not significant in any of the sessions, all $t(7) < 1.72$, all $p > .129$, except for Session 4, $t(7) = 2.55$, $p \leq .05$. Neither the main effect Session nor the Session × Hand were significant, both $F(4, 28) < 1.17$, both $\eta_p^2 < .143$.

Second, incompleteness of intermanual transfer was investigated by comparing randomization costs for the sequence hand with transfer benefits for the random hand, that is, measures of sequence learning with the sequence hand and of intermanual transfer with the random hand defined relative to performance on baseline trials with the respective hand. In order to make costs and benefits comparable, both measures were computed by subtracting median RTs on structured trials from median RTs on random trials. Incompleteness of intermanual transfer would be confirmed in this analysis, if the amount of sequence learning as reflected in randomization costs was higher than the amount of intermanual transfer as reflected in transfer benefits. Indeed, randomization costs were significantly higher than transfer benefits in each session, all $t(15) > 3.84$, all $p \leq .005$. This expressed itself as a significant main effect Hand, $F(1, 15) = 52.51$, $p \leq .001$, $\eta_p^2 = .829$, in a Session × Hand (sequence hand vs. random hand) repeated-measures ANOVA on RT costs/benefits. The main effect Session was also significant, $F(4, 60) = 68.75$, $p \leq .001$, $\eta_p^2 = .821$. The Session × Hand interaction was not significant, $F(4, 60) = 1.94$, $p \leq .146$, $\eta_p^2 = .114$, $\varepsilon_{GG} = .658$. An analogous Session × Hand ANOVA on error costs/benefits revealed no significant effects, all $F < 1.11$, all $\eta_p^2 < .069$.

Analyses Not Restricted to the Second Half of Blocks. The same set of analyses performed on mean RTs and PEs computed from data from all trials of each block confirmed all the major findings reported above, all relevant $p \leq .05$ (for relevant means see Figure 21): Sequence learning increased over the course of the experiment. Correspondingly, intermanual

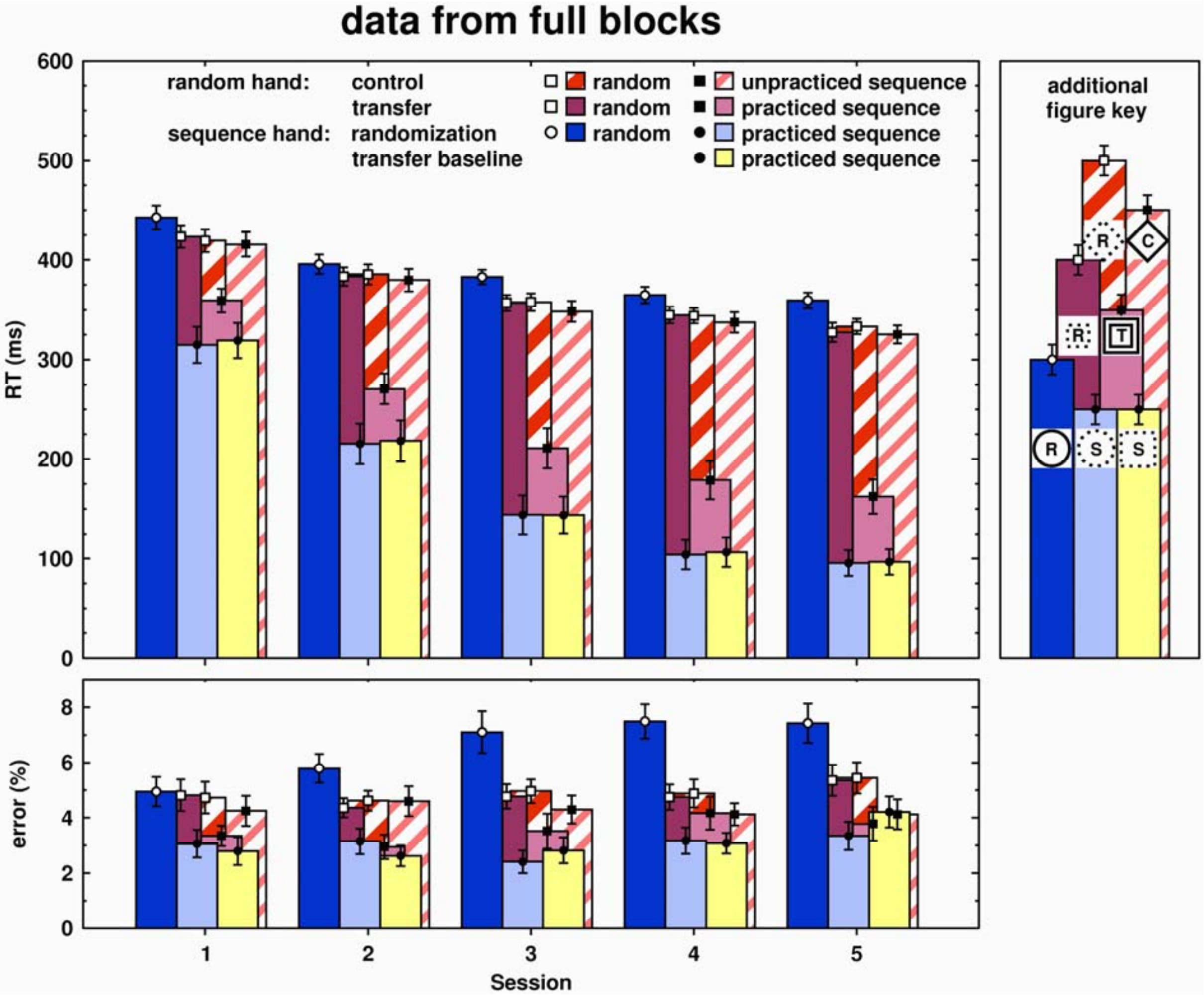


Figure 21. Means of individual median RTs and error rates in the various types of test and baseline blocks separately for the five sessions in Experiment 6. Data from all trials were included. Error bars represent standard errors of the means. *Note.* For the additional figure key (cf. Figure 19), each type of test block is represented by a different shape drawn with a solid line (circle = randomization test block [R]; square = transfer test block [T]; diamond = control condition test block with unpracticed structured sequence [C]). Blocks serving as baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. S/T = practiced structured sequence block; R = random sequence block; C = unpracticed structured sequence.

transfer also increased over the course of the experiment. Some within-block learning of the unpracticed sequences occurred, but not enough to invalidate the intermanual transfer interpretation. Finally, despite the considerable amount of intermanual transfer, a non-transferable component of sequence knowledge was evident in all sessions.

An additional Session × Hand × Block Half (first half, second half) ANOVA on RTs showed in form of a significant Hand × Block Half interaction, $F(1, 15) = 30.98$, $p \leq .001$, $\eta_p^2 = .674$, that the comparison between the sequence hand and the random hand in terms of RTs for responding to the practiced structured sequence yielded a significantly more pronounced assessment of the effector-specific sequence component of sequence knowledge in the first block half ($M_{\text{struc\_hand}} = 174.6$ ms vs. $M_{\text{rand\_hand}} = 249.3$ ms) than in the second block half ($M_{\text{struc\_hand}} = 180.1$ ms vs. $M_{\text{rand\_hand}} = 226.6$ ms). This confirms that restricting analyses to data from the second half of each block did indeed constitute the more conservative test for incompleteness of intermanual transfer.

Sequence Recall Task. Nine participants recalled the practiced sequence completely. The remaining 7 participants exhibited considerable fragmentary explicit knowledge of the practiced sequence by recalling a mean number of 7.14 corresponding triples (out of 12; *SD* = 1.86). The fact that participants were so much aware of the sequence was not surprising considering the very short RTs produced by participants in structured sequence blocks in later sessions and for which the term reaction time seems a misnomer of sorts as participants were most likely not reacting to imperative stimuli but instead producing the sequence of key presses in anticipation of the stimuli.

The Role of Explicit Sequence Knowledge. The analyses on data from the second half of blocks were repeated for the sub-sample of twelve participants who displayed only fragmentary explicit sequence knowledge. Due to the reduced sample size (n=7), it was not possible to repeat the analyses involving the between-subjects factor Direction of Transfer. Also related to the small size of the sub-sample and the associated reduction of statistical power, an effector-specific component of sequence knowledge missed significance in sessions 1 and 2 in the analysis on absolute RTs, $p \leq .067$ and $p \leq .054$, respectively, as well as in session 1 in the analysis comparing randomization costs and transfer benefits, $p \leq .080$. Apart from that, the same pattern of results was obtained as for the entire sample.

5.1.3 Discussion

Participants performed in an SRT task, responding in blockwise alternation (a) to a structured repeating sequence of stimuli with one hand and (b) to a random sequence of stimuli with the other hand. Sequence learning and intermanual transfer were assessed in test blocks at the end of each of five sessions.

Compared to performance of random sequences, participants' performance of the structured sequence which they practiced during sequence-hand blocks improved substantially with practice over the course of the experiment, thus indicating increasing sequence learning. A considerable portion of the acquired sequence knowledge was available for intermanual transfer. Nevertheless, responding to the practiced sequence with the other (random) hand never reached the same level of performance as responding with the sequence hand. This finding, which suggests an effector-specific component of sequence knowledge, was obtained although data analysis was biased in favor of intermanual transfer, and although conditions were arranged such that conditions for intermanual transfer should have been optimal: As participants responded to imperative stimuli appearing in identical locations by pressing the exact same keys with homologous fingers of either hand, any sequence knowledge represented in terms of a sequence of stimuli, or in terms of a sequence of keys to be pressed, or even in terms of a sequence of homologous finger movements should have been available for intermanual transfer. And indeed, intermanual transfer was considerable. However, it was not complete.

The effector-specific component of sequence knowledge emerged after relatively little practice and was already evident at the end of the first session after an average of only 120 sequence repetitions. Moreover, the effector-specific component of sequence learning did not increase significantly across sessions, whereas the transferable component of sequence knowledge continued to increase considerably up until session 4. This dissociation further underscores that effector-specific sequence learning and effector-independent sequence learning might indeed rely on separate sequence learning modules. While there have been reports of effector-specific sequence learning after relatively little practice under particular conditions as discussed in the Introduction (Bird & Heyes, 2005; Heyes & Foster, 2002; Osman et al., 2005; Palmer & Meyer, 2000), effector-specificity of sequence learning in an SRT task is usually obtained only after considerably more practice (e.g., Park & Shea, 2005; see also Verwey & Clegg, 2005). How does the experimental setting implemented here differ from or resemble these previous experiments in ways that might have brought about the observed very fast development of effector-specific sequence learning?

Neither the fact that the 110 ms response-stimulus interval (RSI) was somewhat shorter than typical nor the fact that participants exhibited considerable explicit sequence knowledge at the end of the experiment appears to offer viable explanations. An effector-specific component of sequence learning has been observed for a 0 ms RSI (Verwey & Wright, 2004) as well as for a 200 ms RSI (Verwey & Clegg, 2005). As for explicit sequence knowledge, there is no way of knowing whether and to what extent participants already possessed explicit sequence knowledge at the end of session 1 as participants' awareness of the sequence was not assessed at this point in the experiment. If participants were already aware of the sequence towards the end of session 1, it would be even more perplexing that they failed to fully transfer the acquired sequence knowledge.

The most obviously atypical aspect of this setting is that, in between structured blocks, participants responded to random sequences with the transfer hand throughout most of the experiment. This was done in order to ensure that participants practiced the S-R mapping to the same extent with both hands. However, this manipulation might have had unintended consequences as will be discussed next. Recall that sequence learning appears to occur on different representational levels (cf. Clegg et al., 1998): For example, learning might occur in terms of a sequence of stimuli, in terms of a sequence of keys to be pressed, in terms of regularities between responses and the subsequent stimuli (R–S), and even in terms of a sequence of to-be-moved fingers. One might speculate whether the presentation of random blocks alternately with sequence blocks during acquisition might have led to partial extinction of sequence learning on some of these representational levels. In particular, during the interleaved random blocks, participants experienced random sequences of stimuli in the same locations in which the practiced sequence appeared during sequence blocks, and thus pressed in a random sequence the same keys which they had pressed in the practiced sequence during sequence blocks. This entails that practiced R-S regularities are altered as well. Therefore, some extinction of sequence learning on all of these effector-independent representational levels is conceivable. Only effector-specific sequence learning in terms of to-be-moved fingers appears to be exempt from the possibility of extinction because responses during random and during sequence blocks are executed with fingers of different hands. In other words, the acquisition of abstract effector-independent sequence knowledge might be particularly adversely affected by extinction while the acquisition of effector-specific sequence knowledge would be spared. Obviously, any such extinction can only have been partial as sequence learning was very pronounced and intermanual transfer was substantial. Nevertheless, such a differential effect of extinction on different representation levels of sequence learning might have resulted in the effector-specific component of sequence knowledge becoming more prominent and thus emerging after less practice under the conditions as implemented in Experiment 6 than under more conventional conditions. Another possibility is that practice with responding randomly with the transfer hand might interfere with the ability to execute the transferred structured sequence at test.

Another atypical aspect of this setting concerns the fact that participants' peripheral view of the keys was blocked by the key rod. Even though participants looked at the screen while performing the SRT task, this setup might have induced them to conceptualize the task in terms of moving certain fingers in response to certain imperative stimuli instead of responding to certain imperative stimuli by pressing certain keys (although participants were instructed in terms of which key to press for which stimulus location). This in turn might have resulted in sequence learning occurring more in terms of a sequence of fingers to be moved than in terms of a sequence of keys to be pressed, and thus more effector-specific. For Heyes and colleagues experiments on effector-specific sequence learning by observation (Bird & Heyes, 2005; Heyes & Foster, 2002; Osman et al., 2005) it is also true that the view of the keys being pressed was blocked (by the fingers of the model person whom participants observed executing a sequence). Both of these accounts lend themselves to experimental testing and both were tested in Experiment 7.

5.2 Experiment 7

In large parts, Experiment 7 was a replication of session 1 from Experiment 6. The two additional manipulations concerned (a) the blockwise alternation between the sequence and the random hand, and (b) whether participants were provided with an opportunity for a peripheral view of the keys or not. Findings from Experiment 6 should be replicated when conditions are identical (interrupted practice, hidden keys). To the extent that both or only one of the manipulated procedural peculiarities was responsible for the finding of non-transferable sequence knowledge after relatively little practice, the findings from Experiment 6 should not be obtained in Experiment 7 as a function of both or either of the manipulations.

5.2.1 Method

As Experiment 7 was highly similar to Experiment 6 in several respects, only the differences between the two experiments are described here.

Participants. Forty-eight volunteers (mean age 22.2 years) participated in partial fulfillment of course requirements. Again, only participants who reported to be right-handed were recruited.

Task and Design. Unlike Experiment 6, only randomization and transfer test blocks were implemented. The control condition, consisting of blocks in which unpracticed structured sequences appeared for the random hand, was not included. Two new between-subjects manipulations were implemented: One half of participants responded with the sequence and the random hand in blockwise alternation throughout the session as in Experiment 6 (interrupted practice condition), whereas the remaining participants switched to responding with the random hand only for the transfer block and the corresponding baseline blocks (uninterrupted practice condition). Orthogonally to this factor, one half of participants had no view of the keys mounted on the far side of the rod as in Experiment 6 (hidden keys condition), whereas the remaining participants were provided with the opportunity for a peripheral view of these keys (reflected keys condition). Twelve participants were assigned to each of the four cells in the design resulting from crossing these two between-subjects factors. Within each cell, direction of transfer was counterbalanced across participants, except in the reflected keys condition with uninterrupted practice where – due to experimenter error – transfer was from the dominant to the non-dominant hand for 7 participants and from the non-dominant to the dominant hand for 5 participants.

Apparatus and Materials. Providing participants with the opportunity for a peripheral view of the keys in the reflected keys condition was accomplished by placing a small mirror (11 cm wide, 15 cm high) circa 8 cm behind the key rod (from the participants' point of view) so that participants were able to see the keys on the far side of the key rod (as well as their fingers on these keys) in this mirror.

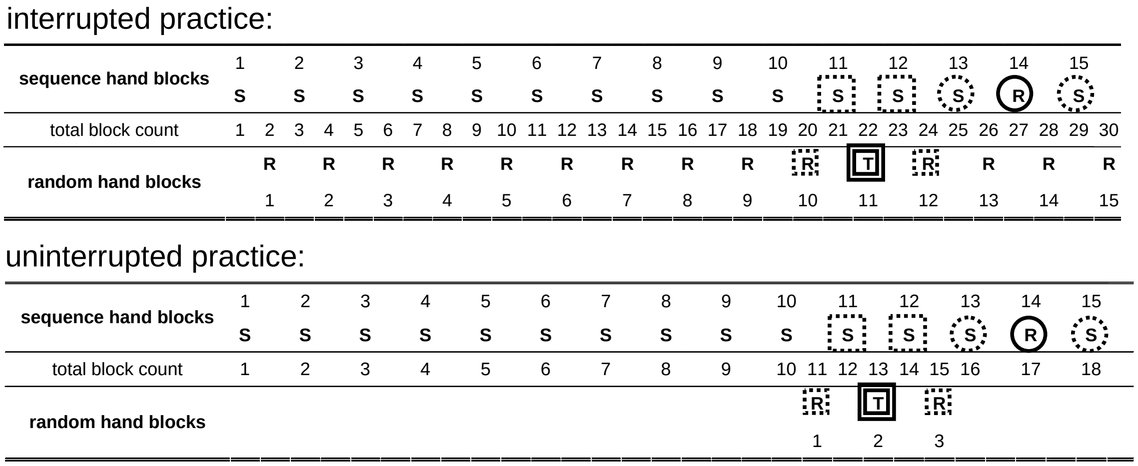


Figure 22. Example of a possible test block schedule in Experiment 7. Each type of test block is represented by a different shape drawn with a solid line (circle = randomization test block [R]; square = transfer test block [T]). Blocks serving as baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. *Note.* S/T = practiced structured sequence block; R = random sequence block.

Procedure. In contrast to Experiment 6, Experiment 7 encompassed only a single session. Participants in the interrupted practice condition completed 30 blocks, 15 with the sequence hand and 15 with the random hand. Participants in the uninterrupted practice condition completed only 18 blocks, 15 with the sequence hand and 3 with the random hand. The ordering of randomization and transfer blocks was counterbalanced across participants. The randomization test block was either the 12th or the 14th sequence-hand block. Accordingly, the transfer block was inserted either prior to the 14th or the 12th sequence-hand block, respectively. In the uninterrupted practice condition, two additional random-hand blocks which served as baseline blocks for the transfer block were inserted before and after the structure-hand blocks immediately preceding and succeeding the transfer block (see Figure 22 for an exemplary illustration). On average, participants completed 144 sequence repetitions prior to the randomization block (not counting sequence repetitions in transfer blocks).

After completing the SRT task, participants were debriefed about the presence of a sequence and its exact length. Then, they were asked to engage in a generation task as described for Experiment 5 with the hand with which they had practiced the sequence. Participants had to generate two sequences each consisting of 96 key presses: one under inclusion and the other under exclusion instructions.

5.2.2 Results

Data were treated as described for Experiment 6. RTs from error trials (4.6 %) and outlier RTs (1.9%) were excluded (interrupted practice, hidden keys: 4.1%, 2.1%; interrupted practice, reflected keys: 5.1%, 1.8%; uninterrupted practice, hidden keys: 4.2%, 1.9%; uninterrupted practice, reflected keys: 5.1%, 1.8%). Unless otherwise noted, RT and PE data were analyzed in Practice Schedule (interrupted vs. uninterrupted) × Keyview (hidden vs. reflected) × Structure Hand Assignment (left hand = structure hand vs. right hand = structure hand) × Blocktype ANOVAs with repeated measures on the last factor. Depending on the test block to be analyzed, median RTs and PEs from that test block and from the corresponding baseline were assigned to the two levels of the Blocktype factor.

Randomization Blocks. Structure-hand RTs were significantly slower on random trials than on structured baseline trials, $F(1, 40) = 198.60$, $p \leq .001$, $\eta_p^2 = .832$. This main effect Blocktype was involved in a significant interaction with Practice Schedule, $F(1, 40) = 7.32$, $p \leq .01$, $\eta_p^2 = .155$, indicating that these randomization costs were significantly more pronounced in the uninterrupted practice condition, $t(23) = 14.43$, $p \leq .001$, than in the interrupted practice condition, $t(23) = 7.13$, $p \leq .001$ (see Figure 23A). There was no comparable effect of the Keyview manipulation on the size of randomization costs, $F(1, 40) = 0.26$, $\eta_p^2 = .003$. Sequence learning tended to be more pronounced with the non-dominant left hand than with the dominant right hand, but the appropriate Sequence Hand Assignment × Blocktype interaction was not significant, $F(1, 40) = 3.36$, $p \leq .074$, $\eta_p^2 = .077$. No other main effects or interactions were significant, all $F(1, 40) < 1.69$, all $\eta_p^2 < .041$.

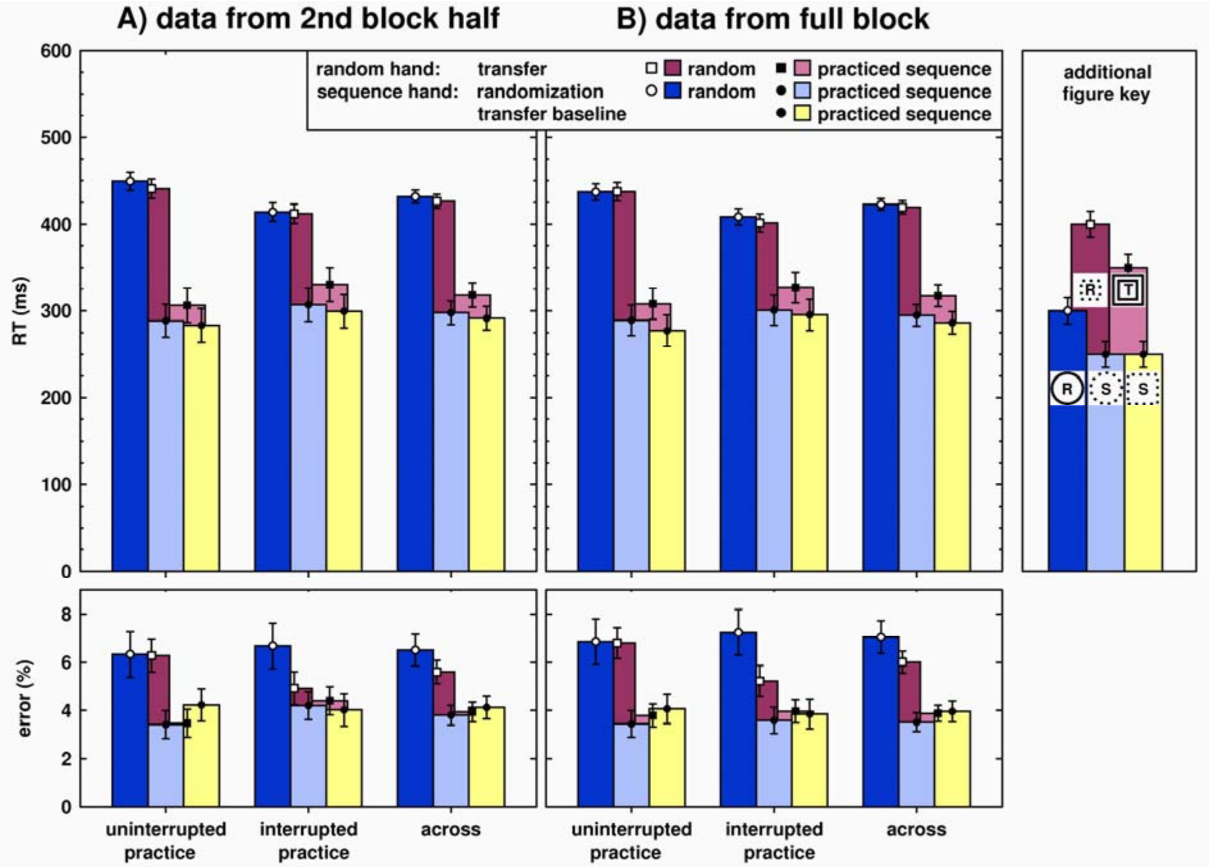


Figure 23. Means of individual median RTs and error rates in the various types of test and baseline blocks separately and across the Practice Schedule conditions in Experiment 7, and separately for data from the second half of blocks (A) and for data from all trials (B). Error bars represent standard errors of the means. *Note.* For the additional figure key (cf. Figure 22), each type of test block is represented by a different shape drawn with a solid line (circle = randomization test block [R]; square = transfer test block [T]). Blocks serving as baseline blocks for these test blocks are indicated by corresponding shapes drawn with a dashed line. S/T = practiced structured sequence block; R = random sequence block.

Similarly, structure-hand PEs were significantly increased on random trials relative to structured baseline trials, $F(1, 40) = 19.56$, $p \leq .001$, $\eta_p^2 = .328$. However, the Blocktype × Practice Schedule interaction was not significant, $F(1, 40) = 0.11$, $\eta_p^2 = .003$. The main effect

Keyview came closest to but did not reach significance, $F(1, 40) = 3.06$, $p \leq .088$, $\eta_p^2 = .071$, as participants in the reflected keys group tended to make more errors ($M = 6.0\%$; $SE = 0.7$) than participants in the hidden keys condition ($M = 4.4\%$; $SE = 0.7$). No other main effects or interactions were significant, all $F(1, 40) < 1.88$, all $\eta_p^2 < .045$.

Transfer Blocks. Intermanual transfer was evident as random-hand RTs were faster on sequence transfer trials than on random baseline trials, $F(1, 40) = 124.84$, $p \leq .001$, $\eta_p^2 = .757$. This main effect Blocktype was involved in a significant interaction with Practice Schedule, $F(1, 40) = 6.56$, $p \leq .05$, $\eta_p^2 = .141$, such that this transfer benefit was significantly larger in the uninterrupted practice condition, $t(23) = 8.79$, $p \leq .001$, than in the interrupted practice condition, $t(23) = 7.17$, $p \leq .001$. Again, there was no comparable Keyview × Blocktype interaction, $F(1, 40) = 0.05$, $\eta_p^2 = .001$. The four-way interaction came closest to but did not reach significance, $F(1, 40) = 3.04$, $p \leq .089$, $\eta_p^2 = .071$.The other main effects and interactions were not significant either, all $F(1, 40) < 2.77$, all $p > .104$, all $\eta_p^2 < .065$.

Intermanual transfer was also evident in lower random-hand PEs in transfer block than in baseline blocks, $F(1, 40) = 15.39$, $p \leq .001$, $\eta_p^2 = .278$, and again significantly moderated by Practice Schedule, $F(1, 40) = 7.30$, $p \leq .01$, $\eta_p^2 = .154$: The transfer benefit was significant only in the uninterrupted practice condition, $t(23) = 4.02$, $p \leq .001$, but not in the interrupted practice condition, $t(23) = 1.18$, $p \leq .250$. No other main effects or interactions were significant, all $F(1, 40) < 1.88$, all $\eta_p^2 < .045$.

Completeness of Intermanual Transfer. A Practice Schedule × Keyview× Structure Hand Assignment × Hand (structure hand vs. random hand) ANOVA revealed that despite considerable intermanual transfer responding to the practiced structured sequence was still significantly slower with the random hand than with the sequence hand, $F(1, 40) = 24.66$, $p \leq .001$, $\eta_p^2 = .381$. Unlike the amount of sequence learning and the amount of intermanual transfer, the size of this non-transferable, effector-specific component of sequence knowledge was not influenced by Practice Schedule, $F(1, 40) = 0.51$, $\eta_p^2 < .013$.

Participants in the group practicing the structured sequence with the non-dominant left hand tended to be generally faster than participants in the other group, but this main effect was not significant, $F(1, 40) = 3.34$, $p \leq .075$, $\eta_p^2 = .377$. The other main effects and interactions were not significant either, all $F(1, 40) < 1.40$, all $\eta_p^2 < .034$. No significant effects were observed in an analogous ANOVA on PEs, all $F(1, 40) < 1.65$, all $p > .157$, all $\eta_p^2 < .040$.

The same results were obtained in analyses restricted to the sub-sample of participants for whom the structured sequence was transferred from the non-dominant to the dominant hand: Random-hand RTs (*M* = 297.0 ms; *SE* = 16.4) were significantly slower than sequence-hand RTs (*M* = 268.1 ms; *SE* = 15.3), *F*(1, 21) = 15.13, *p* ≤ .001, η_p^2 = .419. No other main effects or interaction were significant, all *F*(1, 21) < 1.87, all *p* > .186, all η_p^2 = .082.

In an analogous ANOVA on PEs, the main effect Keyview came closest to but did not reach significance, *F*(1, 21) = 3.10, *p* ≤ .093, η_p^2 = .129, as participants in the reflected keys group tended to make more errors (*M* = 4.6%; *SE* = 0.5) than participants in the hidden keys condition (*M* = 3.2%; *SE* = 0.5). All other main effects and interactions were not significant either, all *F*(1, 21) < 0.98, all η_p^2 < .045.

A Practice Schedule × Keyview × Structure Hand Assignment × Hand ANOVA on measures of sequence learning with the sequence hand and of intermanual transfer with the random hand defined relative to performance on baseline trials with the respective hand confirmed the finding of a non-transferable component of sequence knowledge: Randomization costs (*M* = 132.5 ms; *SE* = 9.4) were significantly higher than transfer benefits (*M* = 106.3 ms; *SE* = 9.5), *F*(1, 40) = 12.27, *p* ≤ .001, η_p^2 = .235. Moreover, costs/benefits were generally higher in the uninterrupted practice condition (*M* = 144.3 ms; *SE* = 12.3) than in the interrupted practice condition (*M* = 94.5 ms; *SE* = 12.2), *F*(1, 40) = 8.21, *p* ≤ .01, η_p^2 = .170. There was no significant interaction between these two factors, *F*(1, 40) = 0.02, η_p^2 < .001. Indeed, randomization costs were significantly higher than transfer benefits both in the uninterrupted practice condition, *t*(23) = 2.48, *p* ≤ .05 (M_{sequence} = 160.6 ms; *SE* = 11.1; M_{transfer} = 134.3 ms; *SE* = 15.3), and in the interrupted practice condition, *t*(23) = 2.53, *p* ≤ .05 (M_{sequence} = 107.0 ms; *SE* = 15.0; M_{transfer} = 81.9 ms; *SE* = 11.4). Again, the main effect Sequence Hand Assignment approached but did not reach significance, *F*(1, 40) = 3.61, *p* ≤ .065, η_p^2 = .083, as costs/benefits tended to be higher in the group of participants practicing the structured sequence with the non-dominant left hand than in the other group of participants. No other main effects or interactions were significant, all *F*(1, 40) < 2.22, all η_p^2 < .053.

In an analogous Practice Schedule × Keyview × Structure Hand Assignment × Hand ANOVA on error costs/benefits the main effect Practice Schedule approached but did not reach significance, *F*(1, 40) = 3.03, *p* ≤ .089, η_p^2 = .070, as benefits tended to be generally higher in the uninterrupted practice condition (*M* = 2.9%; *SE* = 0.6) than in the interrupted practice condition (*M* = 1.5%; *SE* = 0.5). The other main effects and interactions were not significant either, all *F*(1, 44) < 2.06, all *p* > .159, all η_p^2 < .049.

Analyses Not Restricted to the Second Half of Blocks. The same set of analyses performed on median RTs and PEs computed from data from all trials of each block largely confirmed the findings reported above, all relevant $p \leq .05$ unless otherwise noted (for relevant means see Figure 23B): Both sequence learning and intermanual transfer was significantly more pronounced in the uninterrupted practice condition than in the interrupted practice condition. Despite considerable intermanual transfer, a non-transferable component of sequence knowledge was also evident in the analyses on absolute RTs. The analyses on costs/benefits also showed a significant non-transferable component of sequence knowledge not only for RT data, but also for PE data, $F(1, 40) = 4.94$, $p \leq .05$, $\eta_p^2 = .110$. Although the interaction between the factors Hand (structure hand vs. random hand) was significant neither for RT data, $F(1, 40) = 1.16$, $p \leq .288$, $\eta_p^2 = .028$, nor for PE data, $F(1, 40) = 3.03$, $p \leq .089$, $\eta_p^2 = .070$, separate pairwise comparisons showed significantly higher randomization costs than transfer benefits only in the interrupted practice condition, RT: $t(23) = 3.54$, $p \leq .005$; PE: $t(23) = 2.90$, $p \leq .01$, whereas this difference missed significance in the uninterrupted practice condition, RT: $t(23) = 1.71$, $p \leq .100$, PE: $t(23) = 0.46$, $p \leq .647$. Finally, the analyses not restricted to data from the second half of each block showed that overall sequence learning was significantly more pronounced in the group of participants practicing the structured sequence with the non-dominant left-hand than in the other group of participants: The following effects which approached significance in the main analyses were now significant: The Practice Schedule × Keyview × Structure Hand Assignment × Blocktype (randomization vs. structured baseline) ANOVA on structure-hand RTs revealed a significant Sequence Hand Assignment × Blocktype interaction, $F(1, 40) = 5.51$, $p \leq .05$, $\eta_p^2 = .121$. The Practice Schedule × Keyview× Structure Hand Assignment × Hand (structure hand vs. random hand) ANOVA on RT costs/benefits main effect yielded a significant main effect Sequence Hand Assignment, $F(1, 40) = 4.38$, $p \leq .05$, $\eta_p^2 = .099$.

Generation Task. Participants' performance in the generation task was scored and analyzed as described for Experiment 5. Due to experimenter error, generation task data were not available from one participant in the reflected keys condition with uninterrupted practice.

Participants produced more corresponding triples under inclusion than under exclusion conditions, $F(1, 43) = 54.29$, $p \leq .001$, $\eta_p^2 = .558$. Also, participants in the uninterrupted practice group produced more corresponding triples than participants in the interrupted practice group, $F(1, 43) = 5.99$, $p \leq .05$, $\eta_p^2 = .122$. The interaction between these two factors was not significant, $F(1, 43) = 2.51$, $p \leq .121$, $\eta_p^2 = .055$. The other main effects and interactions were not significant either, all $F(1, 44) = 0.39$, all $\eta_p^2 < .009$. Relevant means are given in Table 10.

An index of the amount of acquired explicit sequence knowledge was obtained by subtracting the number of corresponding triples produced by a participant under exclusion conditions from the number of corresponding triples produced by the same participant under inclusion conditions. The sample was split along the median (17 corresponding triples) of this score. The 24 participants classified as possessing fragmentary explicit sequence knowledge produced on average 5.6 (*SE* = 1.4) more corresponding triples under inclusion than under exclusion conditions, $t(23) = 4.08$, $p \leq .001$, whereas the remaining participants – classified as possessing substantial explicit sequence knowledge – produced on average 35.6 (*SE* = 3.1) more corresponding triples under inclusion than under exclusion conditions, $t(22) = 11.36$, $p \leq .001$.

The Role of Explicit Sequence Knowledge. The sub-sample of participants possessing fragmentary explicit sequence knowledge consisted of 9 and 15 participants from the uninterrupted and interrupted practice conditions, respectively. At the same time, this sub-sample included 11 and 13 participants from the reflected and hidden keys condition, respectively. The number of participants in each cell of the crossed design ranged from a minimum of 3 to a maximum of 8, rendering any interactions involving both of these factors obtained in the analyses restricted to this sub-sample un-interpretable. Also, the reduced size of this sub-sample meant that it made no sense to include the additional between-subjects factor Structure Hand Assignment in the analyses restricted to this sub-sample. The analyses restricted to the sub-sample of participants possessing fragmentary explicit sequence knowledge revealed the same pattern of results as the analyses for the entire sample.

Table 10
Mean number of corresponding triples (standard error of the mean in parentheses) produced in the post-experimental sequence generation task in Experiment 7 separately for as well as across the instruction conditions and the practice schedule conditions.

	Instructions		
Practice Schedule	inclusion	exclusion	mean
uninterrupted	58.38 (4.18)	33.56 (2.70)	45.97 (2.90)
interrupted	44.04 (4.09)	28.00 (2.64)	36.02 (2.84)
mean	51.21 (2.92)	30.78 (1.89)	

5.2.3 Discussion

Participants performed in an SRT task under one of two practice schedules: Either they responded in blockwise alternation (a) to a structured repeating sequence of stimuli with one hand and (b) to a random sequence of stimuli with the other hand as in Experiment 6 (interrupted practice), or they responded with only one hand to a repeating sequence of stimuli appearing in all blocks. Orthogonally to this manipulation, participants had no opportunity for a peripheral view of the keys as in Experiment 6 (hidden keys condition) or they could see the keys in a mirror (reflected keys condition).

Learning of the structured sequence was observed under both practice schedules, but it was significantly better in the uninterrupted practice condition than in the interrupted practice condition. Accordingly, intermanual transfer was also more pronounced in the former than in the latter condition. Despite considerable intermanual transfer, responding to the practiced sequence with the random hand never reached the same level of performance as responding with the sequence hand. Unlike the amount of effector-independent sequence knowledge, the amount of effector-specific sequence knowledge did not differ between the two practice schedules. So, while the uninterrupted practice schedule interfered with the acquisition of effector-independent sequence knowledge, this appeared to be not case for the acquisition of effector-specific sequence knowledge. This dissociation is consistent with the notion that effector-specific sequence learning and effector-independent sequence learning might indeed rely on separate sequence learning modules. Also, not only was the development of effector-specific sequence knowledge after relatively little practice replicated in Experiment 7, but the use of the interrupted practice schedule can be ruled out as a possible cause for this finding.

An effect of practice schedule was also apparent in performance in the sequence generation task: In agreement with results from randomization probes in the SRT task, participants in the uninterrupted practice condition produced significantly more corresponding triples across inclusion and exclusion instructions than participants in the interrupted practice condition. Furthermore, across both practice schedules, participants produced significantly more corresponding triples under inclusion than under exclusion instruction, thus displaying explicit sequence knowledge. However, the fact that the interaction between these two factors was not significant indicates that the participants in the uninterrupted practice condition did not acquire more explicit knowledge than participants in the interrupted practice condition. Moreover, the obtained pattern of results did not appear to depend on the extent of the acquired explicit sequence knowledge.

The observed detrimental effect on sequence learning of interrupted practice as compared to uninterrupted practice is reminiscent of the contextual-interference effect (e.g., Shea & Morgan, 1979; Simon & Bjork, 2001): When to-be-learned materials or tasks are arranged in a way that is likely to promote interference between different materials or tasks (e.g., practicing materials or tasks in a randomly determined order), acquisition is typically impeded, but subsequent retention is oftentimes enhanced, relative to practice arrangements that minimize interference during acquisition (e.g., blocked practice). Here, interrupted practice is likely to have caused interference and has indeed impeded acquisition of effector-independent sequence knowledge relative to uninterrupted practice. Future studies should investigate (a) whether interrupted practice in the SRT task as implemented here also leads to better retention of effector-independent sequence knowledge than uninterrupted practice, and, even more interesting, (b) whether effector-specific sequence knowledge is exempt from the contextual-interference effect on retention, which seems possible given the lack of an interference effect on acquisition of effector-specific sequence knowledge observed here. If confirmed, this would further validate the notion that effector-specific sequence learning occurs in separate modules for different effectors.

In contrast to the practice schedule manipulation, the keyview manipulation influenced neither sequence learning nor intermanual transfer significantly. This manipulation was introduced based on the consideration that the key rod setup might promote the fast development of effector-specific learning of a sequence of finger movements, as observed in Experiment 7, because the fact that the keys are effectively hidden from participants might induce them to conceptualize the task in terms of which finger to move instead of which key to press. Providing participants with the opportunity for a peripheral view of the keys in a mirror (reflected keys condition) was believed to counteract this supposed effect of the regular setup (hidden keys condition). Given the lack of evidence for an effect of this manipulation on sequence learning one might be inclined to dismiss this possibility. However, this might be premature. Perhaps the mirror was not suitable for providing participants with an opportunity for a peripheral view of the keys. The tendency of participants in the reflected keys condition to make more errors than participants in the hidden keys condition suggests that participants may have been confused by the mirror.

Another aspect of the experimental setup (vertically aligned keys mounted on a rod) which might account for the fast-developing effector-specific sequence learning observed in Experiments 6 and 7 has yet to be discussed. Participants grip the key rod attached perpendicular to the table top much like they might grab a handle or a stick (see Figure 18), with the index, middle, ring, and little finger on the keys on the far side of the rod and the thumb on the opposite side. Therefore, pressing the keys on the far side might involve the exertion of counter force on the rod with the thumb from the opposite side – although such counter force is not really needed to stabilize the rod as it is firmly attached to the table – so that the task of sequentially pressing keys on the rod is akin to a finger-thumb opposition task. In other words, pressing keys vertically aligned on the rod might involve a greater number of different effector muscles than pressing horizontally aligned keys, and probably requires more elaborate coordination between the involved effector muscles. As a consequence, pressing keys on a rod in a finger-thumb opposition fashion might simply provide more basis for effector-specific sequence learning, which has been suggested to pertain primarily to coarticulatory optimization (e.g., Jordan, 1995; Verwey & Clegg, 2005). This speculation awaits empirical testing.

6 General Discussion

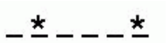
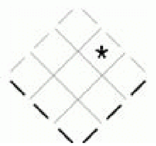
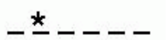
The overall goal of the research presented here was to investigate motor contributions to learning of highly skilled action sequences in contrast to sensory contributions. Of particular interest in Experiments 1–4 was (a) whether two concurrently implemented hand-related sequences would be learned independently of one another as opposed to integrated learning of a compound sequence spanning both hands, and – with regard to the representational format – (b) under which conditions independently acquired hand-related sequence knowledge is such that it is available for intermanual transfer and under which conditions it is specific to the effector used during acquisition and thus non-transferable. Additionally, the acquisition of effector-specific sequence knowledge was also investigated for learning of a single sequence (Experiments 5–7). Previous research has shown that effector-specific sequence knowledge develops primarily after extended periods of practice (e.g., Park & Shea, 2005). Therefore, the experiments involved extensive practice. Experiment 6 in particular was designed to establish the time course of the development of effector-specific sequence knowledge across several practice sessions. An overview of the experiments is given in Table 11.

Experiment 1 constituted a laboratory approximation of real-world tasks requiring coordinated hand movements in response to different aspects of the environment. In a bimanual-bisequential variant of the SRT task, on each trial two imperative stimuli appeared simultaneously, one for each hand, and participants were instructed to respond by simultaneously pressing the two corresponding keys with the appropriate fingers. Left-hand and right-hand stimuli appeared in different fixed repeating sequences so that participants responded in different fixed repeating sequences with the left and the right hand. Participants engaged in extensive practice of this task.

Relative to regular blocks, participants' speed of responding suffered more when both hand-related sequences were randomized than when only one of them was randomized while the other was maintained. Furthermore, in terms of response accuracy, detrimental effects of sequence randomization relative to regular blocks were observed only for that hand which lost its sequence but not for that hand which retained its sequence. This pattern of RT and error costs clearly indicates independent learning of the two hand-related sequences.

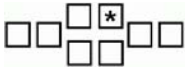
Additional transfer blocks in which left-hand stimuli followed the sequence that was practiced with the right hand while the right-hand stimuli were randomized and vice versa revealed intermanual transfer of the hand-related sequences: RT costs in these transfer blocks were significantly lower than when both sequences were randomized, and error costs were ob-

Table 11
Overview of the experiments in terms of key procedural features and main findings.

Experiment	Stimulus display	Extent of practice prior to test blocks	Sequence characteristics	Test of hand-specificity	Summary of main results
Experiment 1		624 repetitions ... & 520 repetitions ...	of 5-element sequence ... of 6-element sequence; uncorrelated sequences; each defined on 3 positions/keys	transfer of hand-related stimulus sequence to other hand	independent learning of the two sequences; sequence knowledge completely transferable
Experiment 2	 vs. 	720 repetitions ... & 640 repetitions ...	of 8-element sequence ... of 9-element sequence; uncorrelated sequences; each defined on 3 positions/keys	see Experiment 1; independent learning of hand-related sequences despite low visual separability?	independent learning of the two sequences; transferable and non-transferable components of sequence knowledge
Experiment 3		480 repetitions ... & 400 repetitions ...	of 5-element sequence ... of 6-element sequence; uncorrelated sequences; each defined on 3 positions/keys	see Experiment 1; independent learning of hand-related sequences despite temporal separation and low visual separability?	independent learning of the two sequences; non-transferable sequence knowledge
Experiment 4		192 and 392 repetitions …	of two 8-element correlated sequences (each defined on 4 positions/keys) establishing a 16-element compound sequence (defined on 8 positions/keys)	see Experiment 3	integrated learning of the compound sequence and independent learning of its constituent sequences; non-transferable sequence knowledge

(continued of next page)

Table 11 (continued)
Overview of the experiments in terms of key procedural features and main findings.

Experiment	Stimulus display	Extent of practice prior to test blocks	Sequence characteristics	Test of hand-specificity	Summary of main results
Experiment 5		152, 320, and 488 repetitions	8-element sequence; defined on 4 positions/keys; sequence stimuli alternating with random stimuli	responding to sequence stimuli with fingers of one hand only (within-hands assignment) or with fingers from both hands (across-hands assignment)	sequence learning more pronounced under the within-hands assignment than under the across-hands assignment
Experiment 6		120, 288, 456, 624, and 792 repetitions on average	12-element sequence; defined on 4 positions/keys	intermanual transfer under optimal transfer conditions: same sequence of stimuli, response locations, homologous fingers	transferable and non-transferable components of sequence knowledge; the former, but not the latter increasing with practice; non-transferable sequence knowledge evident after relatively little practice
Experiment 7		144 repetitions on average	see Experiment 6	see Experiment 6	transferable and non-transferable components of sequence knowledge after relatively little practice; the former, but not the latter benefits from uninterrupted (compared to interrupted) practice schedule

served only for that hand which responded to a random sequence but not that hand which responded to a transferred sequence. These findings (a) further confirm the conclusion that the hand-related sequences were learned independently of one another, and (b) indicate that this independently acquired sequence knowledge was not specific to the effectors used during practice but relied instead on effector-independent codes.

Independent learning of hand-related sequences in the simultaneous bimanual-bisequential SRT task was replicated in Experiment 2 with longer, more complex sequences and with a further increase in the amount of practice. Moreover, Experiment 2 showed that the acquisition of transferable sequence knowledge depended on the presence of separate stimuli for the two hand-related sequences as intermanual transfer was eliminated in a single-stimulus condition in which only one imperative stimulus indicated both responses. Knowledge about the sequence in which the keys assigned to the respective hand are to be pressed (cf. Willingham et al., 2000) should be as effectively transferable as the order of stimulus locations. In particular, intermanual transfer should not have been complete in Experiment 1 if sequence knowledge in terms of response locations (i.e., keys to be pressed) was not available for intermanual transfer. Thus, the independent knowledge about the hand-related sequences that was observed in this single-stimulus condition must have been based on effector-specific representations. Most likely as a consequence of extended practice, an effector-specific, non-transferable component of sequence knowledge was also evident in addition to a transferable component in the condition with two imperative stimuli.

Independent learning of hand-related sequences persisted also when the two sequences were interleaved so that left-hand and right-hand stimuli appeared in alternation: In Experiment 3, detrimental effects of sequence randomization relative to regular blocks were restricted to that hand which lost its sequence while responding with the hand which retained its sequence was unaffected. It is remarkable that independent learning of the hand-related sequences occurred in spite of the temporal separation as well as the lack of visual separability of the stimuli from each sequence. The only aspect tying together the stimuli belonging to the respective hand-related sequence was that they were consistently responded to with the same hand. As in the single-stimulus condition of Experiment 2, there was no basis for separate stimulus-stimulus (S-S) or response-stimulus (R-S) learning of the two hand-related sequences in Experiment 3. Accordingly and perfectly in line with results from the single-stimulus condition of Experiment 2, there were no indications of intermanual transfer in Experiment 3. Also, there were no indications of integrated learning of the highly complex compound sequence established by the two uncorrelated sequences.

Even when the compound sequence spanning both hands was relatively short and simple – as was the case in Experiment 4 as a result of using interleaved correlated sequences for the two hands – so that integrated sequence learning occurred, partially independent sequence learning was still evident. Significant RT and error costs were obtained for both hands regardless of whether the sequence of only one of the hands or of both hands was randomized, but for each hand randomization costs were higher when it lost its sequence than when it retained its sequence. Moreover, both integrated and independent learning was also evident from results of shift blocks: Shifting the two hand-related sequences relative to each other, so that the practiced compound sequence was destroyed, impaired both response speed and accuracy, thus indicating integrated learning of the compound sequence. However, the effect of sequence shifting on response speed and accuracy was not as detrimental as that resulting from complete randomization of both sequences. This indicates partially independent learning of the hand-related sequences. These findings confirm an effector-related contribution to sequence learning and also suggest that learning of the hand-related sequences in Experiment 3 was not merely a consequence of participants learning the simplest regularities present.

The consistent finding of independent learning of hand-related sequences across several experiments – even in the absence of separate stimuli for the two stimuli, and despite the temporal separation resulting from interleaving the two sequences – bolsters the idea that a separate sequence learning module might exists for each hand (cf. Keele et al., 2003; p. 317). Further support for this notion came from Experiment 5, in which participants responded to stimuli from a sequence either with fingers of one hand only (within-hands assignment) or with fingers of both hands (across-hands assignments). These sequence trials alternated with trials on which participants responded with the remaining fingers to random stimuli. Sequence learning as evident in error costs incurred by randomization probes was more pronounced in the within-hands condition than in the across-hands condition. RT costs did not differ significantly between the assignments.

Experiment 6 was designed as a rigorous test of the possibility that sequence knowledge might be represented as a sequence of finger movements but might still not be effector-specific because it might be transferable to the homologous fingers of the contralateral hand (cf. Deroost et al., 2006; Wachs et al., 1994). Test blocks were implemented in each of five sessions in order to establish a time course of the alleged development of effector-specific sequence knowledge. Unlike Experiments 1–4, in which two sequences were implemented concurrently (either in parallel or interleaved), only one sequence was implemented in Experiment 6. Participants responded to this sequence in a standard SRT task with one of their hands. Sequence practice in regular blocks was interrupted by random blocks in which participants responded with their other hand to a random sequence of stimuli. In order to ensure that participants could comfortably press the same keys with homologous fingers of either hand, response keys were mounted vertically on the far side of a rod attached perpendicular to the table top. Results showed sequence learning with the sequence hand and considerable transfer of acquired sequence knowledge to the other hand. However, intermanual transfer was not complete indicating an effector-specific component of sequence knowledge. This effector-specific component of sequence knowledge was evident after an unexpectedly small number of sequence repetitions and did not increase significantly across sessions. Two procedural peculiarities of the experimental setup were identified as possible reasons for this fast-developing effector-specific sequence learning: (a) the appearance of random stimuli in the same locations as structured stimuli so that the same keys that were pressed in a repeating sequence had to be pressed in a random order might have favored motor-based sequence learning over sequence learning in terms of S-S or R-S learning or in terms of a sequence of response locations; (b) the fact that response keys were effectively hidden from participants' view due to their being mounted on the far side of the rod might have induced participants to conceptualize of the task more in terms of which finger to move than in terms of which keys to press. This, in turn, might have favored hand-specific sequence learning. Both speculations were investigated in the final experiment.

Experiment 7 replicated the early development of effector-specific sequence knowledge observed in Experiment 6 and showed that the interrupted practice schedule was not responsible for this finding: While the amount of acquired effector-independent sequence knowledge was higher in the uninterrupted practice condition than in the interrupted practice condition, the amount of acquired effector-specific sequence knowledge was unaffected by this manipulation. The manipulation either denying or providing participants with the opportunity for a peripheral view of the keys showed no effect. Thus, it remains unclear why effector-specific sequence learning develops so relatively fast under the conditions as implemented in Experiments 6 and 7. Possibly, this occurs because operating the vertically aligned keys on the key rod involves a grip-like hand posture which entails particularly pronounced requirements for coarticulation between consecutive finger movements. Additional empirical investigations will be necessary to resolve this question.

To summarize, at least partly independent learning of two concurrently implemented hand-related sequences was demonstrated after extensive practice under conditions of both simultaneous (Experiments 1 & 2) and alternating (Experiments 3 & 4) stimulus presentation and responding. It persisted when there was only one imperative stimulus for presenting both hand-related sequences (Experiments 2–4) instead of two separate imperative stimuli (Experiments 1 & 2), one for each sequence, even when the hand-related sequences were correlated and massive integrated learning of the compound sequence occurred (Experiment 4). Although low visual separability of the two hand-related sequences (i.e., when there was only a single imperative stimulus for both sequences) did not eliminate independent learning, it did affect the nature of the independently acquired sequence representations such that transferable sequence knowledge was acquired only when there was a separate imperative stimulus for each sequence (Experiments 1 & 2) but not otherwise (Experiments 2–4). The most likely predominantly stimulus-based representations which allow for intermanual transfer can be regarded as sensory components of highly skilled action sequences, whereas motor components can be considered as being reflected in non-transferable sequence knowledge. The same decomposition logic applies to transferable and non-transferable sequence knowledge observed under conditions of unimanual practice of a single sequence (Experiments 6 & 7). The advantage of practicing a key press sequence with fingers of one hand as opposed to using fingers of both hands (Experiment 5) also implicates a motor component as the two assignments were equivalent in all other respects.

While the experiments reported here establish the occurrence of sequence learning on a motor level, they are silent on the issue of whether this motor component of sequence knowledge is represented as a sequence of actual efferent muscle commands or rather in terms of something like an effector-specific sequential motor program for which certain parameters are fixed (e.g., which finger to move or which muscles to use) but others remain freely specifiable (e.g., how much force to exert with that finger or those muscles). These alternatives will have to be teased apart in subsequent experiments. For example, in a test phase including randomization and transfer blocks, participants could be instructed to press the response keys more forcefully than during acquisition. In this way, the sequence in which the muscles have to move is the same but the actual efferent motor commands must be changed to produce the desired increase in exerted force. This manipulation should render useless any non-transferable, effector-specific component of sequence knowledge stored as a sequence of actual efferent motor commands. Observing complete instead of incomplete intermanual transfer as a result of this manipulation would confirm that effector-specific sequence knowledge is stored as a sequence of actual efferent motor commands.

In conclusion, the present series of experiments provides compelling evidence for a motor contribution to sequence learning. Albeit relatively small in size, an effector-specific component of sequence knowledge emerged consistently under various conditions. The findings reported here are in line with the notion that a separate sequence learning module might exist for each hand (cf. Keele et al., 2003; p. 317). Irrespective of which particular theoretical framework these results are incorporated into, it appears that the representation of sequence knowledge is not restricted to higher abstract levels in a hierarchy of movement control, but can also extend to lower levels responsible for the specification and coordination of specific muscle movements. Presumably, the acquisition of effector-specific sequence knowledge serves the purpose of optimizing coarticulation of consecutive movements as an ultimate contribution to refining the execution of sequential actions and attaining high levels of performance.

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8 Summary in German: Zusammenfassung

Die Fähigkeit, Regelhaftigkeiten in der Aufeinanderfolge von Reizen oder Aktionen zu erlernen, ist für den Menschen unverzichtbar dafür, die Effizienz seines Verhaltens zu steigern. Oftmals erfordern Handlungssequenzen den koordinierten Einsatz mehrerer Ausführungsorgane (Effektoren; z.B. linke und rechte Hand beim Klavierspielen). Die Rolle der beteiligten Effektoren für das Erlernen einer Gesamtsequenz bestehend aus Teilsequenzen, die unterschiedlichen Effektoren zugeordnet sind (im Folgenden als effektor-bezogene Sequenzen bezeichnet), ist bislang nicht systematisch untersucht worden.

Ein weithin verwendetes Paradigma zur experimentellen Untersuchung von Sequenzlernen ist die serielle Wahlreaktionsaufgabe (serial reaction time [SRT] task; Nissen & Bullemer, 1987): Typischerweise wird in jedem Durchgang an einer von mehreren Positionen auf dem Bildschirm ein imperativer Reiz dargeboten. Die Probanden sind instruiert möglichst schnell die der angezeigten Position zugeordnete Taste zu betätigen, woraufhin der nächste Durchgang beginnt. Ohne dass die Probanden darüber informiert sind, erscheinen die imperativen Reize in einer sich wiederholenden Sequenz. Der Erwerb von Wissen über diese Sequenz wird – nach einer Lernphase – üblicherweise getestet, indem die Sequenz durch eine Zufallsfolge ersetzt wird, und äußert sich dann dadurch, dass sich die Leistung der Probanden in dieser Testphase verschlechtert (d.h. Reaktionszeiten und Fehlerzahl steigen an) gegenüber ihrer Leistung bei Vorhandensein der geübten Sequenz.

Forschung mit dem SRT-Paradigma hat ergeben, dass Sequenzwissen auf unterschiedlichen Ebenen repräsentiert sein kann (siehe z.B. Clegg, DiGirolamo, & Keele, 1998), zum Beispiel als Wissen über eine Sequenz von Reizen, Antworten, oder herzustellenden Effekten. Eine Reihe von Befunden zeigt, dass erworbenes Sequenzwissen unabhängig vom verwendeten Effektor nutzbar ist (z.B. Keele, Jennings, Jones, Caulton, & Cohen, 1995). Dem gegenüber steht eine wachsende Anzahl von Befunden, die einen Anteil am Sequenzwissen belegen, der an das zum Erwerb des Sequenzwissens verwendete Ausführungsorgan (z.B. linke Hand) gebunden (effektor-spezifisch) und somit nicht für die Sequenzausführung mit einem auf andere Ausführungsorgan (z.B. rechte Hand) nutzbar ist (z.B. Verwey & Clegg, 2005). Das heißt, dass kein (z.B. intermanueller) Transfer dieses Anteils am Sequenzwissen stattfindet. Entscheidend für den Erwerb effektor-spezifischen Sequenzwissens scheint ausgiebige Übung der Sequenz zu sein (z.B. Park & Shea, 2005).

Die vorliegende Arbeit beschäftigt sich mit der Untersuchung nicht-transferierbarer und mithin effektor-spezifischer bzw. motorischer Anteile an der Gedächtnisrepräsentation hochgradig trainierter Handlungssequenzen in Abgrenzung zu transferierbaren Anteilen (insbesondere den auf der Abfolge von externen Reizen basierenden sensorischen Anteilen). Besonderes Interesse galt dabei solchen Handlungssequenzen, die den Einsatz mehrer Effektoren erfordern. Zu diesem Zweck wurde in den Experimenten 1–4 eine Variation der Standard-SRT-Aufgabe eingeführt, bei der gleichzeitig zwei hand-bezogene Sequenzen implementiert wurden, die zusammen eine beide Hände überspannende Verbundsequenz etablieren. Unabhängiges Lernen der beiden hand-bezogenen Sequenzen würde sich so äußern, dass bei Ersetzen nur einer der beiden Sequenzen durch eine Zufallsfolge (d.h. die andere Sequenz bleibt bestehen) eine Abnahme der Leistung sich auf diejenige Hand konzentriert, deren Sequenz aufgehoben wird, während die Leistung mit der anderen Hand weitgehend unbeeinflusst bleibt. Zusätzlich wurde das Auftreten intermanuellen Transfers etwaigen unabhängigen Sequenzwissens getestet durch Verschieben der mit der einen Hand geübten Sequenz auf die andere Hand.

Zumindest teilweise unabhängiges Lernen der hand-bezogenen Sequenzen zeigte sich nach ausgiebiger Übung sowohl bei gleichzeitiger (Experimente 1 & 2) als auch bei abwechselnder (Experimente 3 & 4) Reizdarbietung und Antwortausführung. Es trat nicht nur dann auf, wenn jede der beiden hand-bezogenen Sequenzen durch jeweils einen separaten imperative Reiz angezeigt wurde (Experimente 1 & 2), sondern auch dann, wenn lediglich ein imperativer Reiz vorhanden war, der beide hand-bezogenen Sequenzen anzeigte (Experimente 2–4), selbst dann, wenn die hand-bezogenen Sequenzen korreliert waren und beträchtliches integriertes Lernen der Verbundsequenz stattfand (Experiment 4). Obwohl eine geringe visuelle Separierbarkeit der beiden hand-bezogenen Sequenzen (nur ein imperative Stimulus statt zwei getrennter) das unabhängige Lernen nicht eliminierte, hatte sie einen Einfluss auf die Art der erworbenen Sequenzrepräsentationen: Intermanuell transferierbares Sequenzwissen wurde nur dann erworben, wenn ein getrennter imperativer Reiz für jede der beiden Sequenzen vorhanden war (Experimente 1 & 2), aber nicht sonst (Experimente 2–4). Die höchstwahrscheinlich reiz-basierten Repräsentationen, die intermanuellen Transfer ermöglichen, können als sensorischer Anteil hochgradig trainierter Handlungssequenzen betrachtet werden, wohingegen ein motorischer Anteil sich in nicht-transferierbarem Sequenzwissen widerspiegelt.

Die gleiche Zerlegungslogik gilt für transferierbares und nicht-transferierbares Sequenzwissen beim unimanuellen Erwerb einer einzelnen Sequenz (Experimente 6 & 7). Ausgeprägteres Sequenzlernen bei Ausführen einer Sequenz mit den Finger einer Hand verglichen mit dem Ausführen der Sequenz mit Fingern beider Hände – während mit den jeweils übrigen Fingern in jeweils einem Durchgang zwischen zwei Sequenzdurchgängen auf einen

Reiz aus einer Zufallsfolge reagiert wird (Experiment 5) – weist insofern ebenfalls auf einen motorischen Anteil am Sequenzlernen hin als die beiden Zuordnungen ansonsten äquivalent waren. Die Experimente 6 und 7 zeigten überdies, dass ein hand-spezifischer, nicht-transferierbarer Anteil am Sequenzlernen bereits nach relativ wenig Übung entstehen kann. Bedingung hierfür könnte sein, dass die Aufgabe ein besonders hohes Ausmaß an Koartikulation bei der Ausführung der aufeinanderfolgenden Fingerbewegungen erfordert.

Die vorliegenden Experimente liefern übereinstimmende Belege für einen konsistenten – wenn auch relativ kleinen – effektor-spezifischen, motorischen Anteil am Sequenzwissen. In einem hierarchisch strukturierten System zur Bewegunssteuerung scheint Sequenzwissen also nicht nur auf höheren, abstrakten Ebenen repräsentiert zu sein, sondern auch auf niedrigeren, muskel-nahen Ebenen der Spezifikation und Koordination der einzelnen Bewegungen einer Aktions-Sequenz. Insofern als effektor-spezifisches Sequenzwissen sich auf die optimierte Koartikulation einzelner Bewegungen bezieht, kann es zur Erreichung eines hohen Leistungsniveaus bei der Ausführung sequenzieller Handlungen beitragen.

9 Curriculum Vitae in German: Lebenslauf

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Schulbildung und Studium

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08/98 bis 05/99	Auslandsstudienjahr in den USA (University of Illinois at Urbana-Champaign)
04/02	Abschluss des Studiums mit Note 1,2

Praktika und Berufserfahrung

07/99 bis 10/99	Siemens AG, München: ZT IK 7 Fachzentrum User Interface Design (12-wöchiges Praktikum und anschließende Tätigkeit als Werkstudent)
08/01 bis 10/01	Fraunhofer-Institut für Arbeitswirtschaft und Organisation (IAO), Stuttgart: Marktstrategie-Team Usability Engineering (12-wöchiges Praktikum)
06/02 bis 12/03	wissenschaftlicher Mitarbeiter an der Universität Regensburg (Mitarbeit bei der Konzeption und Implementierung eines online-Seminars für die asynchrone Fernlehre im Internet)
seit 01/04	wissenschaftlicher Mitarbeiter an der Universität Würzburg (Mitarbeiter im DFG-Projekt "Der Erwerb körpereigenen Sequenzwissens beim Training bimanueller Handlungsfolgen")

Publikationen und Tagungsbeiträge

Liste umseitig

sonstige Kenntnisse

SPSS für Windows
E-Prime für Windows XP
Experimental Runtime System (ERTS) für MS-DOS

Grundkenntnisse der objektorientierten Programmierung in Java
Grundkenntnisse LaTex

Würzburg, den 22. Februar 2007

Publikationen

Berner, M. P., & Hoffmann, J. (im Druck). Effector-related sequence learning in a bimanual-bisequential serial reaction time task. *Psychological Research*.

Kiesel, A., Berner, M. P., & Kunde, W. (im Druck). Negative congruency effects: A test of the inhibition account. *Consciousness and Cognition*.

Maier, M. A., Berner, M. P., Hau, R. C., & Pekrun, R. (im Druck). Priming the trait category hostility: The moderating role of trait anxiety. *Cognition and Emotion*.

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Maier, M. A., Berner, M. P., & Pekrun, R. (2003). Directionality of affective priming: Effects of trait anxiety and activation level. *Experimental Psychology*, 50, 116–123.

Tagungsbeiträge

Berner, M. P., & Hoffmann, J. (2006). *Die Rolle von Effektoren für das Erlernen effektorbezogener Sequenzen*. Vortrag auf der 39. Herbsttagung experimentelle Kognitionspsychologie (HexKoP), Braunschweig, 17.–19.11.2006.

Berner, M. P., & Hoffmann, J. (2006). *Handspezifisches Sequenzlernen*. Vortrag auf der 48. Tagung experimentell arbeitender Psychologen (TeaP), Mainz, 26.–29.3.2006.

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Berner, M. P., & Hoffmann, J. (2005). *Effektorspezifisches Sequenzlernen in einer bimanuell-bisequenziellen Wahlreaktionsaufgabe*. Poster auf der 47. Tagung experimentell arbeitender Psychologen (TeaP), Regensburg, 4.–6.4.2005.

Berner, M. P., & Hoffmann, J. (2004). *Effektor-spezifisches implizites Sequenzlernen in einer bimanuell-bisequenziellen Version der seriellen Wahlreaktionsaufgabe?* Vortrag auf der 37. Herbsttagung experimentelle Kognitionspsychologie (HexKoP), Würzburg, 5.–7.11.2004.

Berner, M. P., Maier, M. A., & Hau, C. (2003). *Kongruenz- und Inkongruenzeffekte beim Affektiven Priming: Moderierende Einflüsse der Aktivationsstärke*. Vortrag auf der 45. Tagung experimentell arbeitender Psychologen (TeaP), Kiel, 24.–26.3.2004.