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Expectation-violations in sensorimotor sequences: Shifting from LTM-based attentional selection to visual search

Rebecca M. Foerster^{1,2}, Werner X. Schneider^{1,2}

¹Neuro-cognitive Psychology, Bielefeld University

²Cluster of Excellence 'Cognitive Interaction Technology', Bielefeld University

Corresponding Author:

Rebecca M. Foerster

Neuro-cognitive Psychology

Department of Psychology

Bielefeld University, P. O. Box 100131

D-33501 Bielefeld

Germany

rebecca.foerster@uni-bielefeld.de

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Abstract

Long-term memory (LTM) delivers important control signals for attentional selection. Especially in well-practiced multi-step sensorimotor actions, LTM-expectations have an important role in guiding the task-driven sequence of covert attention and gaze shifts. What happens when LTM-expectations are disconfirmed? Does a sensory-based visual-search mode of attentional selection replace the LTM-based mode? What happens when prior LTM-expectations become valid again? We investigated these questions in a computerized version of the number-connection test. Participants clicked on spatially-distributed numbered shapes in ascending order while gaze was recorded. Sixty trials were performed with a constant spatial arrangement. In 20 consecutive trials, either numbers, shapes, both, or no features switched position. In 20 reversion-trials, participants worked on the original arrangement. Only the sequence-affecting number switches elicited slower clicking, visual search-like scanning, and lower eye-hand synchrony. The effects were neither limited to the exchanged numbers nor to the corresponding actions. Thus, expectation-violations in a well-learned sensorimotor sequence cause a regression from LTM-based attentional selection to visual search beyond deviant-related actions and locations. Effects lasted for several trials and reappeared during reversion.

Introduction

Everyday tasks such as making a cup of tea or inserting a PIN code into a device consist of sequential and object-based sensorimotor actions. Such sensorimotor sequences are accompanied by three types of selection processes. In case of manual actions, the target location of the hand has to be selected to plan and calculate a motor command in order to touch, grasp, or place a target object among other objects. Usually, the hand movement is preceded by one or more saccadic eye movements on the selected locations.¹⁻⁶ These saccades are required to bring visual-spatial information for the ongoing hand movement onto the fovea to process it with high visual resolution⁷. Each saccade is, in turn, obligatorily preceded by a covert attention shift.^{8,9} But how do we sequentially select where-to-attend-to, where-to-look-at, and where-to-act-on in a sensorimotor task?

When performing an object-based sensorimotor sequence in an unknown environment, the agent must search through the environment in order to find the relevant target object for each action step of the sequence.¹⁰ When making a tea in a new office kitchen, for example, you have to search for the location of the tea bags before inserting one into your cup. During the visual search for the tea bag, (sub)action-relevant tea bag features are attentionally prioritized by the attentional template within a fixation.¹¹ Locations containing the highest attentional priority have the highest probability of becoming the next saccade target.^{12,13} After having saccaded to a location, it has to be verified whether the fixated region indeed contains the searched object - the tea bag. If not, covert and overt attention shifts are repeated until the target object is finally fixated. Next, the hand movement is planned and executed. Afterwards the next subaction of the sensorimotor sequence follows (e.g., filling the cup with water). This again is accompanied by the described visual-search mode of attentional selection.

After having performed a fixed sensorimotor sequence repeatedly in the same environment, expectations have been built about its action-relevant visual and spatial features. If the tea bag is usually located next to the fridge, then attention and gaze can be shifted directly to the location of the tea bag. Thus, long-term memory (LTM) might take over in controlling for the allocation of covert and overt attention. That memory can indeed be used to direct attention in space has been shown in several single-step tasks.¹⁴⁻¹⁶ In the contextual cueing paradigm, a learned target-distractor configuration in a visual-search task leads to faster performance. This indicates that in contextual cueing,¹⁴ attention allocation is controlled by memory. Moreover, in probability cueing, a spatial region that contains a target with higher probability is preferably attended and looked at.^{15,16} Thus, an expectation about where a target will be found can direct attention and gaze in space in single-step tasks. In sensorimotor sequences with

multiple steps, not only one target object has to be found, but a whole sequence of targets. Recently, we demonstrated for a well-learned cup-stacking task that a whole sequence of attention shifts and saccades is controlled by LTM.^{4,17} Similar results have been found elsewhere.^{1,18,19} Thus, when executing such a routine sensorimotor sequence in a known environment, attentional selection seems to be no longer in a visual-search mode. Instead, expectations about target objects seem to be used to control attention in an LTM mode. The conditions when either an LTM-based mode of attentional selection or a sensory-based visual-search mode is applied have not been investigated yet. Providing a first answer to this question is a key goal of this study.

What types of expectations are acquired and involved in LTM-based attentional selection after having learned a sensorimotor sequence? Location information has to be acquired in order to direct covert attention and gaze in space. Other features of action-relevant objects might also be learned for good reasons. For instance, LTM expectations about an object's shape could help to plan the end point locations for eye or hand movements.²⁰ More precision is needed for grasping a needle than a cup. It should also be helpful to remember the features of a saccade target object in crowded environments in order to decide whether the saccade landed indeed on the selected object.

A suitable tool for studying which types of LTM-based expectations for attentional selection are learned and used in sensorimotor sequences is the build-up and the violation of these expectations.²¹ Is the action relevance of expectation violations decisive for modifying the attentional selection mode in a sensorimotor sequence? Does a regression occur from an LTM-based to a visual-search mode of attentional selection when objects are no longer at expected locations? A surprise mode of attentional selection may come into play, too. In such a mode, expectation-discrepant objects are processed more often and longer covertly – attentional capture^{21–25} as well as overtly – oculomotor capture.^{26–34}

In a sensorimotor sequence, expectation-violations may only refer to parts of the sequence (e.g., a certain subaction). Imagine attempting to make tea in a common kitchen, in which a colleague has moved the tea bag to another shelf. You will not find the bag at the expected location. Perseverating with the LTM-guidance of attention is no longer optimal. Therefore, this mode of attentional selection has to be abandoned within the affected subaction of the sensorimotor sequence of tea making. The tea bag's new location has to be searched for. However, what happens after the bag has been found? Does the LTM-expectation violation in one subaction (handling the tea bag) introduce enough uncertainty to also disturb the LTM-based selection for objects of other subactions such as picking up the tea cup at a certain

location in the shelf? The colleague might have also moved the cups. Does it even introduce enough uncertainty to cause you to recheck whether you really took the intended tea bag?

Given an attentional perspective to sensorimotor sequences, a further interesting question is, what happens to the attentional selection mode in a sequential task (e.g., tea making), if action-irrelevant features (e.g., color of cups in the common kitchen) or irrelevant objects (e.g., position of a plate) change. Such changes are not relevant for the task at hand, so LTM-based selection might still be optimal. Usually, action-irrelevant features and objects are nearly completely ignored when executing sensorimotor sequences.^{2-4,35} However, action-irrelevant changes can signal an unpredictable environment and may thus introduce uncertainty about the validity of LTM-expectations. Moreover, features without relevance for one subaction might become relevant for another subaction. Thus, it is possible that action-irrelevant feature and object changes may also modify the attentional selection mode.

Finally, from a learning perspective on attentional selection in a sensorimotor sequence, the following question is important: what happens when an unexpected feature of an action-relevant object in a well-learned sensorimotor sequence becomes permanent (e.g., cups stay in a new shelf)? Participants could incorporate the change into LTM and use their updated LTM to select where-to-attend and -look next. To the best of our knowledge, only one study investigated the repeated appearance of an expectation-discrepant nonspatial feature on attentional selection, namely a deviant word style in a dot-localization task. Expectation updating of the nonspatial feature was fast, i.e. after the first violation.³⁶ However, spatial-attention biases in other single-step tasks such as probability cueing are very robust and relearning is slow.^{15,16} This preservation of spatial biases might generalize to sequential sensorimotor tasks that are characterized by a sequence of learned spatial-attention shifts.^{4,17} Therefore, not only the first appearance of a target object at a new location - location deviant, but also deviant repetitions might result in a modified attentional selection mode such as visual search. It is unknown how long it takes to update spatial LTM for attentional selection in sensorimotor sequences. The same holds for the reinstatement of spatial LTM for attentional selection after the reappearance of an initially learned task configuration. Is it possible to reinstate a prior LTM-selection mode?

To answer the aforementioned questions, we adopted a computerized version of the number-connection test. Participants clicked on spatially distributed and numbered target objects of various shapes in ascending order (1-8) as fast as possible. During 60-prechange trials, the overall spatial configuration, as well as the visual and spatial features of the target objects, remained the same (Fig. 1). In consecutive 20-change trials, the overall spatial

configuration was kept constant, but the positions of numbers 3 and 6 were interchanged. Importantly, this action-relevant position interchange requires a change in the sensorimotor sequence of hand and eye. In three further experimental conditions, the action-irrelevant shapes of numbers 3 and 6, the location of numbers 3 and 6 with their shapes (the whole objects), or no features were exchanged. In 20-reversion trials, participants worked on the original visuospatial configuration. Throughout, eye movements served as proxies of covert attentional selection.^{8,9} Fixations were categorized depending on their selection function for the current subaction of the sensorimotor sequence. First, searching fixations are required to find the current target.¹ Second, guiding fixations are used to prepare the hand movement to the current target^{4,10,17,37} (also known as sequence¹ or directing² fixations). Third, checking fixations determine whether a condition is met (e.g., whether a target is still present after an expectation violation (surprise)).^{2,10} How might these three types of fixations be distributed in a well-practiced sensorimotor sequence? It seems reasonable to assume for well-practiced sequential sensorimotor actions that as many guiding fixations as action targets (8) should be observed, while searching and checking fixations should hardly be made when an LTM-based mode of attentional selection is applied.^{1,4,17} Classifying these three fixation types should reveal whether the attentional control is in a LTM mode, a visual search mode, or in a check-after-surprise mode after the expectation-violations specified above (number, shape, or object position exchange).

Method

Participants

Forty right-handed students (14 male, 26 female, 25 years on average) from Bielefeld University, Germany, participated. All had normal or corrected-to-normal visual acuity and were naïve with respect to the purpose of the study.

Apparatus and Stimuli

The experiment was controlled by the Experiment Builder software (SR Research, Ontario, Canada). The stimuli were displayed on a 19-inch color monitor with a 100-Hz refresh rate and a resolution of 1024 x 768 pixels. The computer mouse and keyboard and an extra-large mouse pad (32 x 88 cm) were used. An EyeLink 1000 desktop-mounted eye tracker (SR Research) recorded participants' right gaze positions with 1000 Hz. Participants' viewing distance was fixed at 71 cm with a chin-and-forehead rest.

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All stimuli were displayed on a gray background. The mouse cursor was a black dot with a diameter of approximately 0.45° of visual angle (v.a.). The target stimuli consisted of eight black numbers (bold type Arial, font size 35), each displayed on an individual black shape with a diameter of 2.18° v.a. The center of the screen contained a black plus of 0.45° v.a. width and height. The spatial distribution of the eight numbered objects with varying shapes was constant. It was designed by randomly choosing locations on the screen with the prerequisite that each outer field of an imagined 3×3 grid contained one object and objects had a minimal distance of 2.18° v.a. to each other as well as to the screen border. For the generated configuration, the minimal distance between two objects happened to be 7.20° v.a. (between 1 and 4). While all features of objects 1, 2, 4, 5, 7, and 8 stayed in the same location throughout the experiment, positions as well as shapes (circle and plus) of numbers 3 and 6 interchanged for some participants and trials (see the section “Procedure” and Fig. 1).

Procedure

Participants read an instruction on the screen stating that they had to click on numbered shapes in ascending order as fast as possible. In the subsequent nine-point eye-tracking calibration and validation procedure, only calibrations with averaged accuracy below 1.0° v.a. were accepted. The experiment consisted of a 60-trial prechange/acquisition phase, a 20-trial change phase, and a 20-trial reversion phase. Throughout prechange/acquisition phase, all numbered shapes were located at the same position. In the change phase, features could switch depending on the experimental group (Fig. 1). The 40 participants were equally divided into four experimental groups. In the *shape*-change group, the shapes of numbers 3 and 6 (i.e., the plus and the circle) were interchanged. In the *number*-change group, the numbers 3 and 6 switched positions without their shapes. In the *object*-change group, the numbers 3 and 6 switched positions together with their shapes. In the *no*-change group, no changes were introduced. During the reversion phase, the display was exactly the same as during prechange. To control for varying difficulties of trajectories, all odd-numbered participants began with the plus 3 in the upper right position and the circle 6 in the lower left position, while all even participants began with the switched position of plus 3 and circle 6. The experiment started with an example prechange trial.

A click was counted as correct within a diameter of 3.27° v.a. around a target's center. An incorrect click was followed by a low-pitched tone. After all eight objects were clicked sequentially in the correct order, trial-completion time was shown by a feedback display. Each trial was preceded by a central fixation on a black ring (0.48° v.a. outer size, 0.12° v.a. inner

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size) for checking calibration. Calibration was repeated if necessary. After every block of 10 trials, a display informed participants about the number of blocks completed of the total number of blocks. Participants started a block and a trial by pressing the space bar. All participants completed the experiment within 40 minutes. The participant with the fastest best time won a coffee voucher.

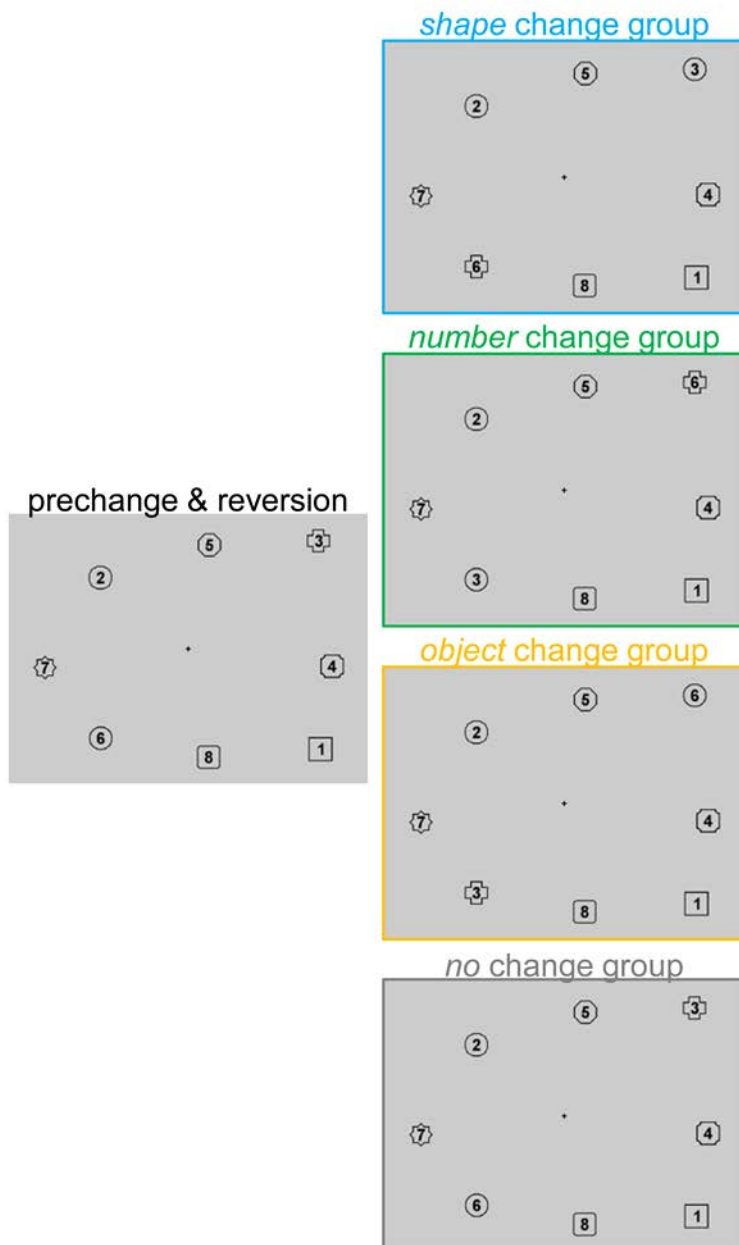


Figure 1. Display during the clicking task in the prechange (left), change (right), and reversion (left) phase of the experiment for the odd participants of the four change groups (*shape-*, *number-*, *object-*, *no-change*). Even participants started with the plus 3 in the lower left position and the circle 6 in the upper right position.

Analysis

The SR Research Data Viewer software's implemented algorithm was used to detect fixations.³⁸ The following variables were analyzed as dependent variables: trial-completion times, number and size of errors, number and duration of fixations, scanpath and cursor-path lengths, and eye-cursor distances. Error size was measured as the Euclidean distance in ° v.a. from the incorrectly clicked location to the actual target's center. Scanpath and cursor-path length were calculated as 100-Hz cumulative intersample distances. Eye-cursor distances were calculated as 100-Hz intrasample distances. For prechange analyses, analyses of variance (ANOVAs) with the within-subject variable block (1-6) were calculated over all groups. For the change analyses, ANOVAs were calculated with change group (*shape, number, object, no*) as between-subject variable and phase (prechange, change, reversion) as within-subject variable. For fine-grained analyses, further within-subject variables were subaction (1-8), location (1-8), and fixation type (searching, guiding, checking). Guiding fixations were defined as fixations to the numbered shape that was the current clicking target (also known as sequence¹ or directing^{2,10} fixations). Checking fixations were defined as fixations to numbered shapes that had already been clicked correctly. Searching fixations were defined as fixations to numbered shapes that had not yet been clicking targets. Fixations were counted as falling on a stimulus within 3.27° v.a. around it. Violations of sphericity were corrected using Greenhouse-Geisser ϵ (uncorrected degrees of freedom are provided to facilitate reading). A chance level of 0.05 was applied.

Results

This section is divided into three parts. First, we report about performance improvements during the prechange/acquisition phase ensuring that participants adopted LTM-based attentional selection for the sensorimotor sequence. Second, we report the effects of different expectation-violation manipulations on performance and eye movements as well as on the three fixation types (searching, guiding, checking), allowing conclusions about the modes of attentional selection (e.g., LTM vs. visual search). Third, we report how the sensorimotor sequence will be updated by the repeated expectation violations, as well as how the prior sensorimotor sequence will be reinstated by showing the previously learned visuospatial task configuration and how this affects the mode of attentional control.

Acquisition of a sensorimotor sequence: effects on attentional selection

Over the course of the six prechange/acquisition blocks, trial-completion times and number of fixations per trial decreased significantly (trial-completion time: $F(5,195) = 52.97$, $\varepsilon = 0.52$, $P < 0.001$, $\eta_p^2 = 0.58$, linear trend $P < 0.001$; number of fixations: $F(5,195) = 55.39$, $\varepsilon = 0.62$, $P < 0.001$, $\eta_p^2 = 0.59$, linear trend $P < 0.001$; Fig. 2). Also cursor-path length, scanpath length, and eye-cursor distance decreased significantly (Supporting Information), while fixation duration had a quadratic trend ($F(5,195) = 3.27$, $\varepsilon = 0.47$, $P < 0.05$, $\eta_p^2 = 0.08$, quadratic trend $P < 0.05$; Fig. 2). In terms of errors, number of errors per trial increased ($F(5,195) = 11.97$, $\varepsilon = 0.58$, $P < 0.001$, $\eta_p^2 = 0.24$, linear trend $P < 0.001$; Fig. 2). However, error size, (i.e., the distance of incorrect clicks to the actual target) decreased with learning (Supporting Information) and achieved a distance of 5.56° v.a. to the actual target in block 6 which is less than the distance between the nearest two circles (7.20° v.a. between 1 and 4). This indicates that late errors are due to incorrect motor parameters and not inaccurate target selection. In sum, participants learned the overall configuration of numbered shapes. The increase instead of a decrease in errors (not in error size) is likely due to the high-speed instruction of the task, making participants the more risky the smaller the best time is they have to beat (e.g., Ref. 4). None of the variables showed significant differences between blocks 5 and 6. Thus, it will be possible to reveal any effects of expectation violations on top of continued sensorimotor refinement.

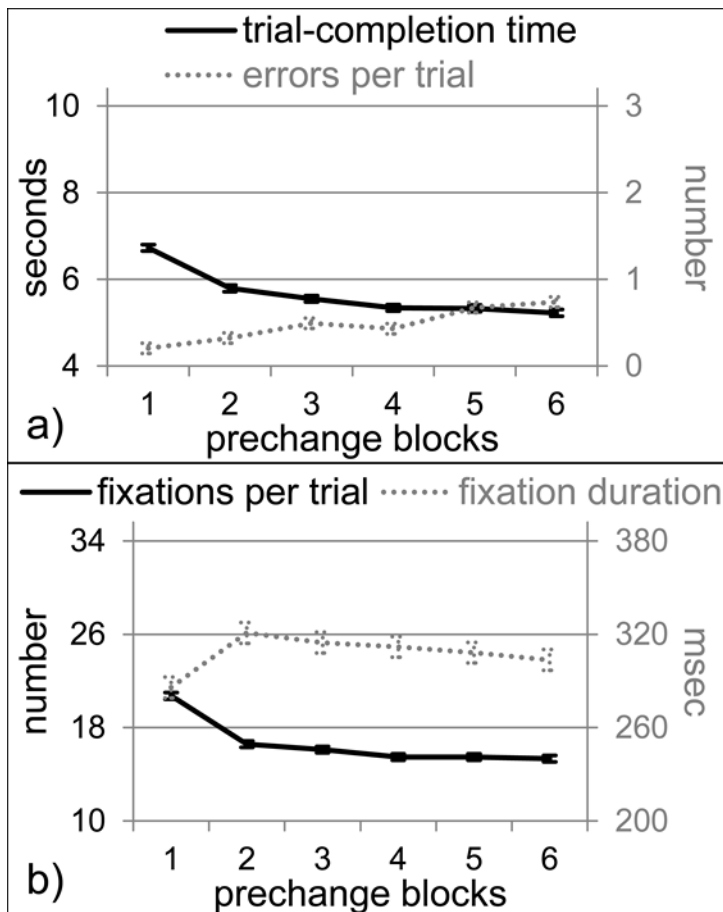


Figure 2. (a) Trial-completion time (black solid line and left y-axis), number of errors per trial (grey dotted line and right y-axis) per prechange block. (b) Number of fixations per trial (black solid line and left y-axis), and fixation duration (grey dotted line and right y-axis) per prechange block. Error bars represent standard errors of the mean, according to Ref. 47.

Disturbance of a sensorimotor sequence: effects on attentional selection

How is LTM-based attentional selection affected by expectation violations that differ in terms of relevance for the required action? We calculated mixed-design ANOVAs for all dependent variables with change group (*number*, *shape*, *object*, *no*) as between-subject factor and phase (prechange, change) as within-subject factor. The prechange baseline consisted of the last block's average (here and elsewhere, alternative baselines do not change the overall result patterns). The first change trial (61) was compared to prechange baseline. Mean values per phase and group can be seen in Figure 3 and Figure S2. There are significant interactions between group and phase for trial-completion time ($F(3,36) = 3.50$, $P < 0.05$, $\eta_p^2 = 0.23$), number of fixations ($F(3,36) = 7.05$, $P < 0.01$, $\eta_p^2 = 0.37$), fixation duration ($F(3,36) = 9.28$, $P < 0.001$, $\eta_p^2 = 0.44$), cursor-path length, scanpath length, eye-cursor distance, and size of errors (Supporting Information), but not for number of errors ($F(3,36) = 0.10$, $P = 0.96$, $\eta_p^2 = 0.01$). Paired *t*-tests per group (Table 1) revealed that in the *number*- and *object*-change groups, fixation duration decreased significantly from prechange to change, while all other

significant variables increased. None of the dependent variables changed from prechange to change in the *no*-change group and also not in the *shape*-change group.

Table 1. Statistics of paired *t*-tests per experimental group comparing prechange to change for all dependent variables.

| | <i>Shape</i> change | <i>Number</i> change | <i>Object</i> change | <i>No</i> change |
|---------------------|------------------------------|-------------------------------|-------------------------------|------------------------------|
| Completion time | $t(9) = 0.63,$ $P = 0.55$ | $t(9) = 3.03,$ $P < 0.05$ | $t(9) = 2.57,$ $P < 0.05$ | $t(9) = 0.31,$ $P = 0.77$ |
| Number of errors | $t(9) = 0.33,$ $P = 0.75$ | $t(9) = 0.39,$ $P = 0.71$ | $t(9) = 0.57,$ $P = 0.58$ | $t(9) = 0.74,$ $P = 0.48$ |
| Error size | $t(4) = 0.74,$ $P = 0.48$ | $t(4) = 6.18,$ $P < 0.01$ | Not enough cells | $t(3) = 1.82,$ $P = 0.17$ |
| Number of fixations | $t(9) = 1.04,$ $P = 0.33$ | $t(9) = 4.16,$ $P < 0.01$ | $t(9) = 3.49,$ $P < 0.01$ | $t(9) = 0.52,$ $P = 0.62$ |
| Fixation duration | $t(9) = 0.61,$ $P = 0.55$ | $t(9) = 3.85,$ $P < 0.01$ | $t(9) = 6.68,$ $P < 0.001$ | $t(9) = 0.34,$ $P = 0.74$ |
| Cursor-path length | $t(9) = 0.33,$ $P = 0.75$ | $t(9) = 2.73,$ $P < 0.05$ | $t(9) = 3.88,$ $P < 0.01$ | $t(9) = 0.29,$ $P = 0.78$ |
| Scanpath length | $t(9) = 0.79,$ $P = 0.45$ | $t(9) = 3.69,$ $P < 0.01$ | $t(9) = 3.98,$ $P < 0.01$ | $t(9) = 0.93,$ $P = 0.38$ |
| Eye-cursor distance | $t(9) = 0.80,$ $P = 0.44$ | $t(9) = 6.07,$ $P < 0.001$ | $t(9) = 4.33,$ $P < 0.01$ | $t(9) = 0.23,$ $P = 0.82$ |

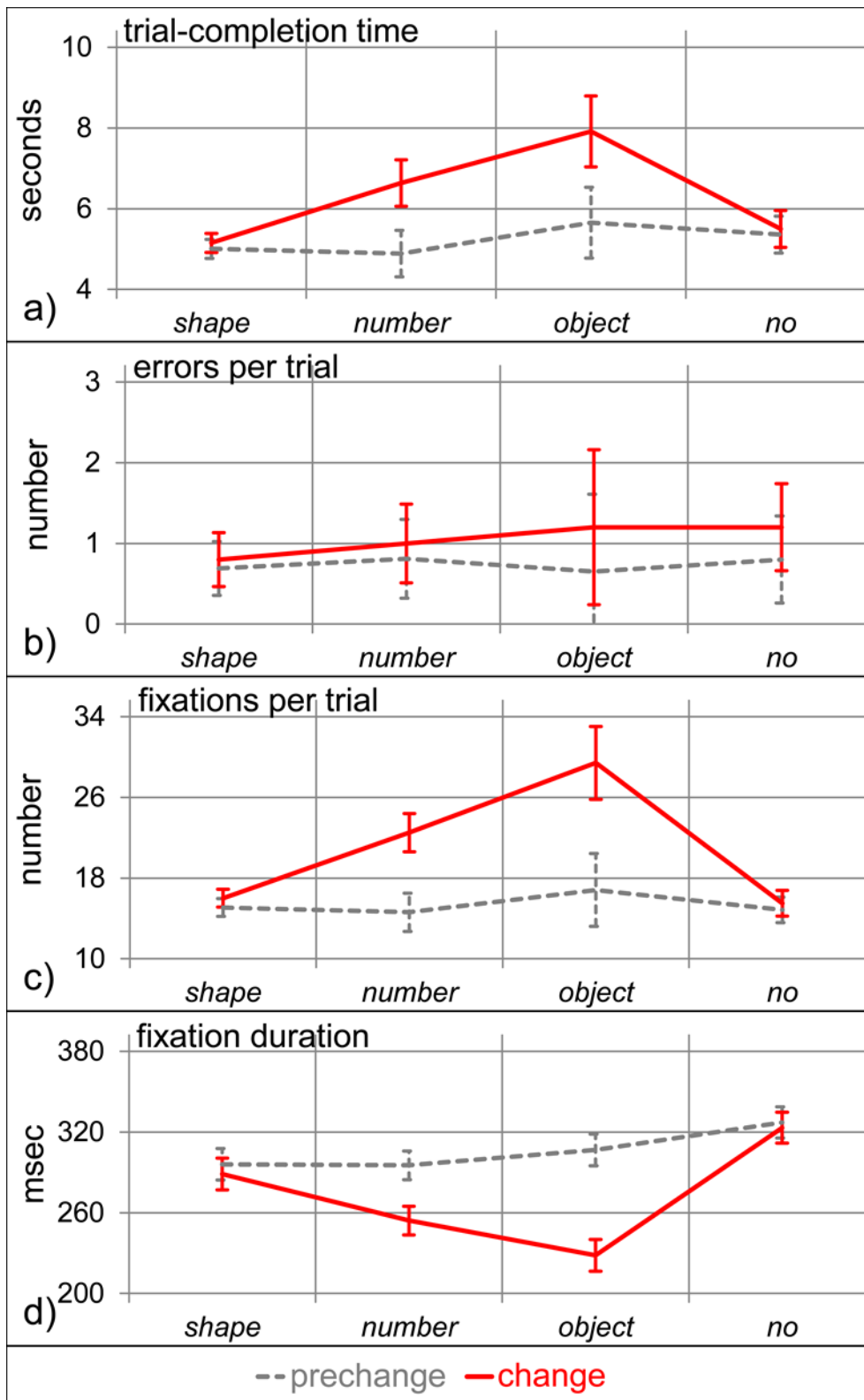


Figure 3. (a) Trial-completion time, (b) number of errors per trial, (c) number of fixations per trial, and (d) fixation duration per phase (prechange, change) and change group (*shape*, *number*, *object*, *no*). Error bars represent standard errors of the mean of the paired differences between prechange and change per group.

We tested whether the size of the change effect differed in the *number*- and *object*-change group by comparing the differences from prechange to change across the two groups with

between-subject *t*-tests. Only the difference values of fixation duration were significantly different across groups (fixation duration: $t(18) = 2.36$, $P < 0.05$; time: $t(18) = 0.43$, $P = 0.63$; number of fixations: $t(18) = 1.15$, $P = 0.27$; cursor-path length: $t(18) = 0.41$, $P = 0.89$; scanpath length: $t(18) = 1.45$, $P = 0.17$; eye-cursor distance: $t(18) = 0.12$, $P = 0.91$). Comparing absolute change values across these groups did not reveal any significant differences (Supporting Information). Because the change effects were not qualitatively (and mostly not quantitatively) different across these two groups, we aggregated the *number*- and *object*-change groups into a common *sequence*-change group in all further analyses. In summary, only the sequence-relevant exchange of the numbers 3 and 6, but not the sequence-irrelevant exchange of the shapes of numbers 3 and 6, affected attentional selection significantly. This expectation violation led to a regression of performance and gaze parameters to a prelearning level (statistics in Supporting Information).

Which mode of attentional selection is used after LTM-expectation violations? To reveal whether a visual-search mode of attentional selection was used after the sequence-relevant change, we investigated number and duration of searching, guiding, and checking fixations (Fig. 4). We compared means of the first change trial to the prechange baseline. Repeated measures ANOVAs with phase (prechange, change) and fixation type (searching, guiding, checking) as within-subject factors were conducted. The analysis for number of fixations revealed significant main effects of fixation type ($F(2,38) = 89.23$, $\varepsilon = 0.69$, $P < 0.001$, $\eta_p^2 = 0.82$) and phase ($F(1,19) = 23.97$, $P < 0.001$, $\eta_p^2 = 0.56$) as well as a significant interaction between phase and fixation type ($F(2,38) = 21.49$, $\varepsilon = 0.77$, $P < 0.001$, $\eta_p^2 = 0.53$). The interaction was due to the fact that more searching fixations were performed during change than during prechange ($t(19) = 7.31$, $P < 0.001$), while the number of guiding and checking fixations were not significantly affected (guiding: $t(19) = 0.26$, $P = 0.80$; checking: $t(19) = 1.81$, $P = 0.09$; Fig. 4). As only six of the 20 participants performed checking fixations in both prechange baseline and change trial, the analysis for fixation duration was performed without checking fixations. The interaction between phase and type of fixation was not significant ($F(1,19) = 0.30$, $P = 0.59$, $\eta_p^2 = 0.02$), nor was the main effect of phase ($F(1,19) = 1.32$, $P = 0.27$, $\eta_p^2 < 0.07$). However, there was a significant main effect of type ($F(1,19) = 31.15$, $P < 0.001$, $\eta_p^2 = 0.62$). Searching fixations were of shorter duration than guiding fixations ($t(19) = 5.58$, $P < 0.001$). Thus, the observed shortened mean fixation duration is a by-product of the increase in short-lasting searching fixations only. In sum, the increase in

number of searching fixations implies that participants used a visual-search mode of attentional selection during the change trial.

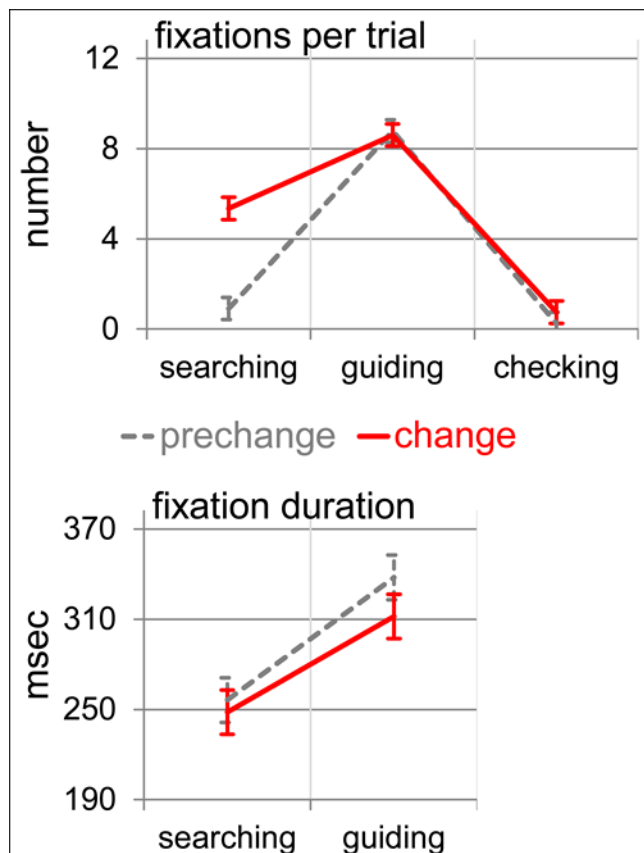


Figure 4. Number of fixations per trial (top) and fixation duration (bottom) per phase (prechange, change) and type of fixation (searching, guiding, checking). Error bars represent standard errors of the mean according to Ref. 47.

Given a regression occurred to the visual-search mode after an expectation violation has been detected, how will selection look like further on in the sequence? Will the search mode continue after the subtraction on the deviant object has been completed? We performed a repeated measures ANOVA for all affected dependent variables with phase (prechange, change) and click action (1-8) as within-subject factor. As a substitute for trial-completion time on a within-trial level, click-completion time was calculated. A target's click-completion time was defined as the time (in milliseconds) from the click on the last target until the click on the current target. Click-completion time of the first target was the time from trial onset to the click on the first target. The analysis for click-completion time revealed significant main effects for click action ($F(7, 133) = 10.62$, $\varepsilon = 0.34$, $P < 0.001$, $\eta_p^2 = 0.36$) and phase ($F(1, 19) = 15.12$, $P < 0.01$, $\eta_p^2 = 0.44$) and a significant interaction ($F(7, 133) = 10.97$, $\varepsilon = 0.37$, $P < 0.001$, $\eta_p^2 = 0.37$; Fig. 5). Paired t -tests revealed that click-completion time was only increased for click actions 3 ($P < 0.001$) and 6 ($P < 0.05$), which

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are actions on deviants. Cursor-path length showed a similar pattern (Supporting Information). The analysis for number of searching fixations revealed also significant main effects of click action ($F(6, 114) = 20.85, \varepsilon = 0.42, P < 0.001, \eta_p^2 = 0.52$) and phase ($F(1, 19) = 53.43, P < 0.001, \eta_p^2 = 0.74$) and a significant interaction ($F(6, 114) = 19.74, \varepsilon = 0.48, P < 0.001, \eta_p^2 = 0.51$; Fig. 5). The number of searching fixations was significantly increased during click actions 3 ($P < 0.001$) and 4 ($P < 0.01$). Main effects and interaction also reached significance for scanpath length and eye-cursor distance (Supporting Information). Scanpaths were elongated during click actions 3, 4, and 6. Eye-cursor distance was increased during click actions 3, 4, 5, 6, and 8 (Supporting Information). There was no significant interaction between click action and phase for the number of errors (Fig. 5; $F(7, 133) = 1.02, \varepsilon = 0.22, P = 0.36$), nor did any main effect reach significance (phase: $F(1, 19) = 0.50, P = 0.49$; click action: $F(7, 133) = 1.28, \varepsilon = 0.22, P = 0.29$). There were not enough valid cases to perform a phase-by-click action analysis for error size. In summary, the visual-search mode of attentional selection was applied as soon as the first deviant became the action target. LTM-based attentional selection was not immediately reinstated after having finished the deviant-related action.

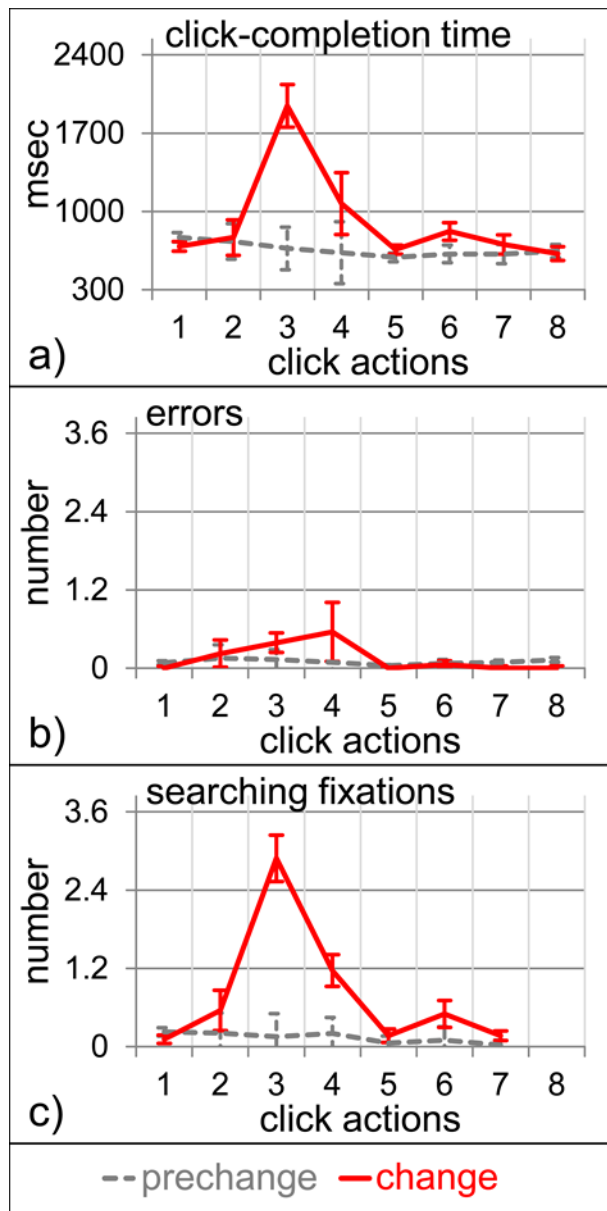


Figure 5. (a) Click-completion time, (b) number of errors, and (c) number of searching fixations per phase (prechange, change) and click action (1-8). Error bars represent standard errors of the mean of the paired differences between prechange and change per click action.

Which target locations did participants select during the search mode? We investigated which locations were fixated on during visual search. We conducted a repeated measures ANOVA for the number of searching fixations with phase (prechange, change) and location (2-8) as within-subject variables. The analysis revealed significant main effects of location ($F(6, 114) = 7.32$, $\varepsilon = 0.28$, $P < 0.001$, $\eta_p^2 = 0.28$) and phase ($F(1, 19) = 44.80$, $P < 0.001$, $\eta_p^2 = 0.70$) as well as a significant interaction between phase and location ($F(6, 114) = 5.80$, $\varepsilon = 0.45$, $P < 0.01$, $\eta_p^2 = 0.23$). The interaction was due to significantly more searching fixations on locations 4-6 and 8 ($ps < 0.05$) but not on locations 2 ($P = 0.48$), 3 ($P = 0.24$), and 7 ($P =$

0.06). Thus, participants searched on nearly all not-yet-clicked locations without specific preferences for any location.

Do participants apply a surprise mode of attentional selection indicated by checking fixations? The overall number of checking fixations was only marginally enhanced during change ($P = 0.09$, also see above), but we also analyzed whether participants checked specific locations during specific subactions significantly more often during change than during prechange. Neither the interaction between phase (prechange, change) and click action ($P = 0.82$), nor the interaction between phase and location reached significance ($P = 0.30$). None of the locations were checked significantly more often during change than during prechange, not even location 3 ($P = 0.32$). Locations 6 and 7 were checked even less often during change than during prechange ($ps < 0.05$). Correspondingly, throughout click actions, participants did not perform more checking fixations during change than during prechange, not even during deviant-concerned click actions 3 ($P = 0.29$) or 6 ($P = 0.44$). In sum, our results do not provide reliable evidence for a surprise mode after an expectation violation.

Updating and reinstatement of a sensorimotor sequence: effects on attentional selection

How long does it take to update an attention-guiding LTM sequence when the expectation violation in the sequence becomes permanent? We calculated paired t -tests for all affected dependent variables comparing each of the first 10 change trials (61-70) to the prechange baseline. Trial completion was decelerated in trials 61, 62, and 65. Error size was higher in trial 61. Cursor-paths were elongated during trials 61 and 63 and scanpaths were elongated during trials 61-63, 65, and 69. Fixation duration was shorter in the first nine change trials. Interestingly, the number of searching fixations, as well as the eye-cursor distance, was significantly increased in the first 10 change trials. Thus, we also compared the other 10 change trials (71-80) to prechange baseline for these variables. The analysis revealed significantly more searching fixations for trials 71-75 and 79, as well as larger eye-cursor distances for trials 71-75. In summary, it takes more than one trial to update the position of the two items in the LTM sequence in order to use it for attention control.

After reversal to the originally learned sensorimotor sequence, can a prior LTM-sequence for attentional selection be reinstated? We calculated paired t -tests for all dependent variables comparing each of the first 10 reversion trials (81-90) to prechange baseline. Trial-completion time, error size, and cursor-path length were increased in the very first reversion trial only. More searching fixations were performed in trials 81-85.

Correspondingly, fixation duration was decreased in trials 81-85. Scanpaths were elongated in trials 81 and 82. Eye-cursor distance was increased in trials 81-85 and 87-89. In summary, the reappearance of the initially learned sequence evoked the same effects as its disturbance, but for shorter duration. This implies that the prior LTM sequence in our task was reinstated for attentional selection within about five trials.

Discussion

Performing a multistep sensorimotor sequence in an unknown environment is accompanied by a sequence of searches for action-relevant objects and corresponding shifts of covert and overt attention to target-like objects. Imagine, for instance, that you have to search for a cup in a new office kitchen. In this scenario, attentional selection is controlled in a visual-search mode - no previously acquired episodic expectations are available to guide attention in space. Of course, you know from semantic memory where cups can be usually found in a kitchen – scene gist.³⁹⁻⁴¹ However, you do not know where exactly the cups are located in the specific kitchen. When repeating a sensorimotor sequence for a task in the same environment, expectations are formed about action-relevant visual and spatial features of objects. These LTM expectations can later be used to guide covert attention and eye movements directly to action-relevant locations in the environment.^{4,17} In the cup-searching scenario, you immediately look to the shelf containing a desired cup in your home kitchen. In such well-practiced everyday sensorimotor sequences, attentional selection is controlled by an LTM-based mode.^{1,4,17} The conditions when either an LTM-based or a visual-search mode of attentional selection is applied have not been previously investigated. The key goal of this study was to provide a first answer to this question. A suitable tool for studying which types of LTM expectations for attentional selection in a sensorimotor sequence are learned and used is to investigate performance and gaze measures during the build-up and the violation of these LTM expectations.²¹

In this study, the acquisition of LTM expectations for attentional selection in a sensorimotor sequence was implemented by having participants repeatedly perform a computerized version of the number-connection test or trail-making test A with a constant visuospatial configuration of target objects. Participants had to click as fast as possible on a constant arrangement of eight spatially-distributed objects with various shapes in ascending order. After 60 prechange/acquisition trials with the same visuospatial arrangement and sequence, features of two objects switched in three experimental groups. The shapes surrounding the numbers 3 and 6 were exchanged in one group (action-irrelevant change),

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while the numbers 3 and 6 switched positions in another group (action-relevant change). In a third group, the object as a whole was exchanged (numbers with their shapes). No changes were introduced in a control group. These different types of changes were introduced to investigate which kind of expectation violations lead to a disturbance of LTM-based attentional selection. The altered visuospatial input was repeated for 20 trials during the change phase to reveal how long it takes to update LTM for attentional selection. In a final reversion phase, all participants worked on the originally learned visuospatial layout of numbered shapes for 20 trials. Whether and how fast previously acquired LTM expectations for attentional selection can be reinstated was investigated during this final phase.

To make claims about the predominant mode of attentional selection in the different phases of the experiment (prechange, change, reversion), fixations were categorized according to their selection function for the current subaction of the sensorimotor sequence. Searching fixations are required to find the current target.¹ Guiding fixations are used to prepare the hand movement – here cursor movement – to the current target^{4,17,37} (also known as sequence¹ or directing^{2,10} fixations). Checking fixations determine the status of former targets.^{2,10} The classification of the three fixation types can reveal which mode of attentional control is applied before and after the described expectation violations (shape, number, object). A visual-search mode of attentional selection should be accompanied by searching fixations, while an LTM-based mode is accompanied by about as many guiding fixations as action targets (here, eight).

Acquisition and disturbance of LTM-based attentional selection: shifting to a visual-search mode

What types of expectations are acquired and involved in LTM-based attentional selection after having learned a sensorimotor sequence? Results revealed effects in manual action and gaze behavior only after an action-relevant expectation violation – exchange of numbers 3 and 6 with or without their shapes. Clicking was slower, errors had a larger size but were not increased in magnitude, more fixations were performed, and fixations were on average shorter in duration. Effects were due to an increase in searching fixations, indicating that a visual-search mode of attentional control was applied after an action-relevant expectation violation.

Action-irrelevant feature changes (i.e., exchange of the shapes of numbers 3 and 6) did not significantly affect manual performance and gaze control. However, at least numerically, action-relevant changes combined with irrelevant changes seemed to affect performance and gaze more than relevant changes alone. Thus, action-irrelevant features of action targets might

nevertheless be important, as they can be used to verify after a saccade to a target whether the eyes landed indeed on the intended object (e.g., the circle 3). However, here the display was not crowded and objects were widely spaced. Thus, there was no necessity for forming expectations about object shapes while learning the sensorimotor sequence. Therefore, it is not surprising that task-relevant shape changes alone did not modulate LTM-based attentional selection significantly. Instead, the shapes of the action targets might have been effectively ignored, as is often the case with action-irrelevant features in sensorimotor sequences.^{2-4,19,35} Alternatively, the shape changes might have been processed, but did not have the power to introduce enough priority to disturb LTM-based attentional selection. Future studies should clarify whether other action-irrelevant feature changes of target objects (besides shapes) can affect attentional selection.

Action-relevant features – here number locations – have to be attended and are stored to LTM in order to guide attention directly in space.^{1,4,14,15,17} When executing the well- practiced sensorimotor sequence late during the prechange phase in this study, LTM should determine where to attend, look, and act as well as which subactions have to be performed in which sequence. This suggested LTM-based attentional selection mode was verified in our data by a dominance of guiding fixations and a tight eye-cursor coupling (cf. Refs. 1, 4, and 17). After the action-relevant location exchange of numbers 3 and 6, LTM was no longer reliable for predicting the sequence of target locations and hence the sequence of attention and gaze shifts. As a consequence, participants regressed to a sensory-based visual-search mode of attentional selection. Specifically, while having to act on the first deviant-located number 3, they looked at other numbers before they found, verified, and finally moved the cursor to click correctly on the newly located target 3. This behavior resulted in a larger amount of searching fixations, longer scanpaths, and larger eye-cursor distances. However, participants did not look significantly more often at locations that had already been clicked successfully – checking fixations – after having noticed the change. The fact that participants did not search on locations of preceding subactions implies two things: (1) they knew reliably where they had already clicked successfully within a trial from memory, and (2) they relied on the invariability of successfully clicked target locations within an ongoing trial. Note that participants in the present study did not even check the deviant-located number 3 after having clicked on it, although processing the change more intensively would have helped remembering the new location for the next trial. Thus, a check-after-surprise mode of attentional selection with more refixations was not initiated.

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The increase in searching fixations was not limited to click action 3, but extended to click action 4. Thus, even when the unchanged – LTM-based expectation matching – number 4 became the action target, participants searched for the 4 by looking on numbers becoming targets later than the 4. This finding implies that participants did not only regress from a LTM-sequence mode to a visual-search mode of attentional selection for one subaction, they also maintained the search mode after having found the new position of the subaction target 3. Accordingly, they scanned longer paths on the display during click actions 3, 4, and 6. Moreover, the coupling between eye and cursor movements became weaker throughout click actions 3, 4, 5, 6, and 8, i.e., eye and cursor moved in higher temporal asynchrony. Scanpaths were prolonged for more trials than cursor-paths and also to a larger extent. Apparently, the eye moved around more frequently (searching) while the cursor was waiting for verification. Our results imply that if expectations for attentional control are disproved within a subaction of a sensorimotor sequence, then LTM-based attentional selection will be interrupted and visual search will dominate, as during early stages of learning and automatization.

While being in a more sensory-based search mode, participants did not make advanced inferences based on the new visual input, such as predicting that number 3 might be at the old location of number 6 when seeing 6 at the old location of 3. In this case, searching fixations would have been increased only on the location of number 6 (old 3) from which participants would have saccaded directly to the new location of number 3 (old 6). Participants either did not encode the complete new spatial configuration of targets while searching for number 3 or they did not recall it when having to act on the later numbers. Otherwise, effects would have been limited to click action 3. In other words, after the interruption of LTM-based attentional selection, participants did not use potential working memory (WM) information about the locations of not-yet-clicked but already fixated targets, especially number 6.

While effects were not limited to click action 3, effects did not arise before the changed number 3 became the current action target. Overt attention usually serves a just-in-time strategy^{3,19} in sensorimotor sequences. From an attentional-research perspective, the currently relevant features are prioritized. Locations that are important for the current subaction of the sensorimotor sequence are fixated while other locations are not.^{3,4,19} Therefore, it is not surprising that expectation deviants affect gaze strongest while they are the current action target. This idea is also in line with the results of Droll *et al.*¹⁹ In their study, participants had to pick up one brick among several bricks depending on a specified pick-up feature (e.g., red color) and put the brick on one of several conveyer belts depending on a specified put-down feature (e.g., big size). In addition, participants had to detect within-trial feature changes on

the brick after pick-up. Detection rates were higher for currently relevant put-down feature changes than for pick-up feature changes that were no longer relevant.

Updating and reinstatement of LTM-expectations for attentional selection

What happens when violations of LTM-based expectations for covert and overt attention are repeated? In this study, the display with exchanged locations of numbers 3 and 6 reappeared in the next trial. During the repeated LTM-discrepant presentation, clicking was again slower than during prechange for 2-3 trials, and more searching fixations, longer scanpaths, and larger eye-cursor distances were observed for up to 15 trials. The perseveration of these effects is inconsistent with the idea of one-trial schema updating.³⁶ It is more in line with the finding of slow relearning of spatial-attention biases.¹⁵ It is also in line with the perseverations observed in a number of reversal-learning studies.⁴²⁻⁴⁶ Moreover, hand-performance measures were affected for a shorter number of trials than gaze measures. The reason might be that eye-movement measures reveal implicit effects such as the interruption of a sensorimotor procedure, while hand-performance measures might reveal more explicit effects such as semantic schema revision. Whether two processes and time courses can be separated is an empirical question for future studies. Here, attentional selection was affected at least in more than one trial after a first expectation-violation.

Reversion to the originally learned sensorimotor sequence elicited the same effects as the appearance of the expectation-violating target layout, but for fewer trials. This indicates that a previously learned LTM-based attentional selection mode can be reinstated after a few trials. Since all effects reverted to prechange level, the reversion effects seem to be indeed due to the disappearance of the second-learned target layout instead of being just after-effects of the change phase.

Conclusions

LTM-based attentional selection in object-based sensorimotor sequences seems to be disturbed mainly by action-relevant expectation violations. In this study, the action-relevant violation was a sequence-affecting switch of two target locations. This LTM-expectation violation caused an immediate return to regressive gaze strategies, namely to a sensory-based visual-search mode of attentional selection. Once disproven, LTM-based attentional processing was not reinstated (immediately) within an ongoing sequence. Thus, violation of one expectation modulates attentional control beyond the unexpected feature and its corresponding subaction. The validity of all action-relevant expectations seemed to be questioned by the first violation, resulting in a regression from an LTM-based to a visual-

search mode of attentional selection, with searches on all objects and during subsequent subactions. However, there seemed to be confidence that all features of action targets remain constant within an ongoing sequence (trial). Therefore, memory was used to avoid checking prior targets. Finally, complete updating of LTM-expectations for attentional control persisted for several trials.

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Author contributions

R.M.F. designed and programmed the experiment, analyzed, interpreted and discussed the results, and wrote the manuscript. W.X.S. supervised the empirical work, interpreted and discussed the results, and revised the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

Supporting Information

Additional supporting information may be found in the online version of this article.

Figure S1. (a) Cursor-path length (black solid line and left y-axis), scanpath length (black dashed line and left y-axis), eye-cursor distance (grey dotted line and right y-axis), and (b) error size as distance of erroneous clicks to actual target per prechange block. Error bars represent standard errors of the mean according to Ref. 47.

Figure S2. (a) Cursor-path length, (b) scanpath length, (c) eye-cursor distance, and (d) error size per phase (prechange, change) and change group (*shape, number, object, no*). Error bars represent standard errors of the mean of the paired differences between prechange and change per group.

Figure S3. (a) Cursor-path length, (b) scanpath length, and (c) eye-cursor distance per phase (prechange, change) and click action (1–8). Error bars represent standard errors of the means of the paired differences between prechange and change per click action.

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Supporting Information

Acquisition of a sensorimotor sequence: effects on attentional selection

The following variables decreased over the course of the six prechange trials:

Cursor-path length: $F(5,195) = 52.77$, $\varepsilon = 0.71$, $P < 0.001$, $\eta_p^2 = 0.58$, linear trend $P < 0.001$

Scanpath length: $F(5,195) = 49.03$, $\varepsilon = 0.67$, $P < .001$, $\eta_p^2 = 0.56$, linear trend $P < 0.001$

Eye-cursor distance: $F(5,195) = 5.22$, $\varepsilon = 0.50$, $P < 0.01$, $\eta_p^2 = 0.12$, linear trend $P < 0.001$

Error size: $F(5,110) = 3.57$, $\varepsilon = 0.55$, $P < 0.05$, $\eta_p^2 = 0.14$, linear trend $P < 0.05$

Means are shown in Fig. S1.

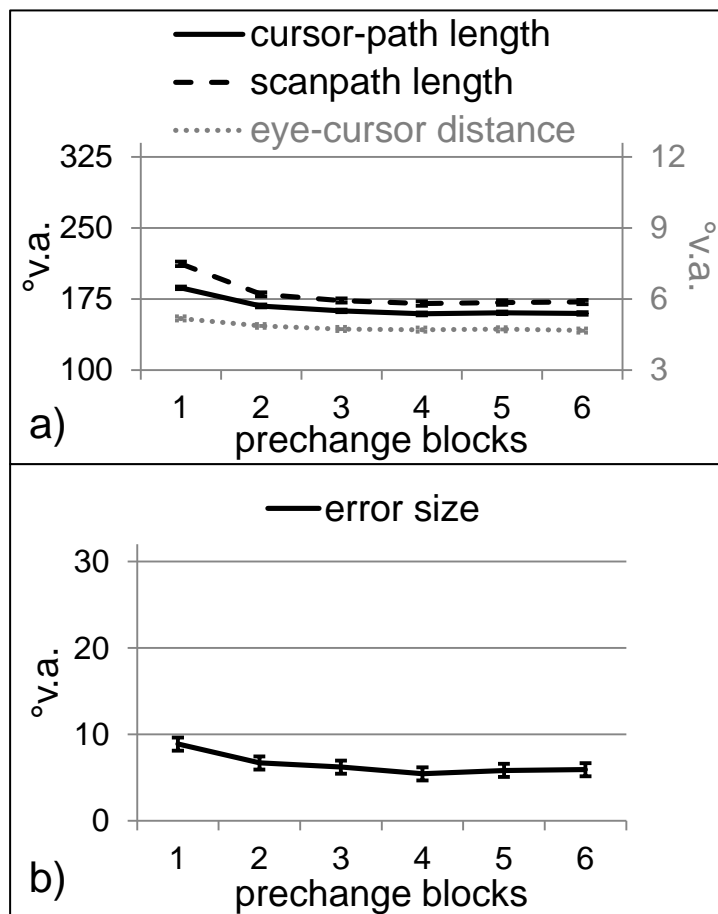


Figure S1. (a) Cursor-path length (black solid line and left y-axis), scanpath length (black dashed line and left y-axis), eye-cursor distance (grey dotted line and right y-axis), and (b) error size as distance of erroneous clicks to actual target per prechange block. Error bars represent standard errors of the mean according to Loftus and Masson (1994).

Disturbance of a sensorimotor sequence: effects on attentional selection

There were significant interactions between group (*shape, number, object, no*) and phase (prechange block 6, change trial 61) for these variables:

Cursor-path length: $F(3,36) = 5.39$, $P < 0.01$, $\eta_p^2 = 0.31$

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Scanpath length: $F(3,36) = 8.45$, $P < 0.001$, $\eta_p^2 = 0.41$

Eye-cursor distance: $F(3,36) = 13.26$, $P < 0.001$, $\eta_p^2 = 0.53$

Error size: $F(3,11) = 12.99$, $P < 0.01$, $\eta_p^2 = 0.78$

Means are shown in Fig. S2.

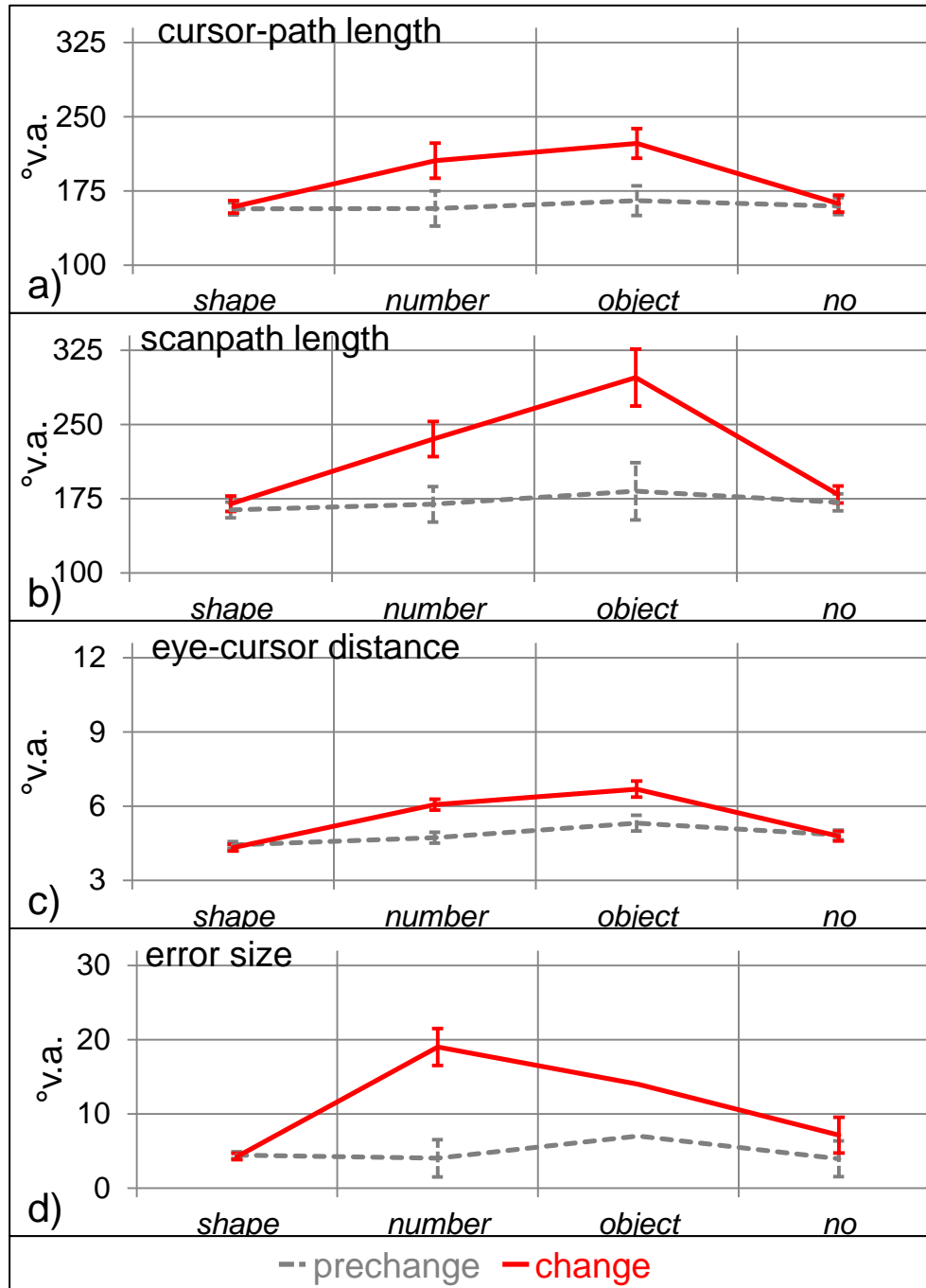


Figure S2. (a) Cursor-path length, (b) scanpath length, (c) eye-cursor distance, and (d) error size per phase (prechange, change) and change group (*shape*, *number*, *object*, *no*). Error bars represent standard errors of the mean of the paired differences between prechange and change per group.

LTM-based attentional selection vs. visual search

None of the absolute change values was significantly different across *number-* and *object-* change groups (time: $t(18) = 1.12$, $P = 0.28$; number of fixations: $t(18) = 1.48$, $P = 0.16$; fixation duration: $t(18) = 1.71$, $P = 0.10$; cursor path length: $t(18) = 0.79$, $P = 0.44$; scanpath length: $t(18) = 1.80$, $P = 0.09$; eye-cursor distance: $t(18) = 1.31$, $P = 0.21$).

There were no significant differences across change (trial 61) and prelearning (trial 1):

Trial-completion time: 7.27s change to 7.87s prelearning $t(19) = 0.99$, $P = 0.33$

Number of fixations: 25.95 change to 26.85 prelearning $t(19) = 0.35$, $P = 0.73$

Fixation duration: 241.26ms change to 253.54ms prelearning $t(19) = 1.14$, $P = 0.27$

Cursor-path length: 6.48°v.a. change to 7.04°v.a. prelearning $t(19) = 1.27$, $P = 0.22$

Scanpath length: 8.04°v.a. change to 8.16°v.a. prelearning $t(19) = 0.17$, $P = 0.87$

Eye-cursor distance: .19°v.a. change to .18°v.a. prelearning $t(19) = 1.05$, $P = 0.31$

Error size: Not enough valid cells to perform the analysis.

There were significant main effects of phase (prechange, change) and click action (1-8):

Cursor-path length:

Click action main effect: $F(7,133) = 25.41$, $\varepsilon = 0.50$, $P < 0.001$, $\eta_p^2 = 0.57$

Phase main effect: $F(1,19) = 21.94$, $P < 0.001$, $\eta_p^2 = 0.54$

Click action by phase interaction: $F(7,133) = 11.94$, $\varepsilon = 0.41$, $P < 0.001$, $\eta_p^2 = 0.39$

Increased during click action 3 ($P < 0.001$) and marginally during 6 ($P = 0.06$).

Scanpath length:

Click action main effect: $F(7,133) = 19.64$, $\varepsilon = 0.56$, $P < 0.001$, $\eta_p^2 = 0.51$

Phase main effect: $F(1,19) = 26.85$, $P < 0.001$, $\eta_p^2 = 0.59$

Click action by phase interaction: $F(7,133) = 19.87$, $\varepsilon = 0.49$, $P < 0.001$, $\eta_p^2 = 0.51$

Increased during click actions 3 ($P < 0.001$), 4 ($P < 0.05$), and 6 ($P < 0.05$)

Eye-cursor distance:

Click action main effect: $F(7,133) = 17.00$, $P < 0.001$, $\eta_p^2 = 0.47$

Phase main effect: $F(1,19) = 51.73$, $P < 0.001$, $\eta_p^2 = 0.73$

Click action by phase interaction: $F(7,133) = 3.35$, $\varepsilon = 0.43$, $P < 0.05$, $\eta_p^2 = 0.15$

Increased during click actions 3 ($P < 0.001$), 4 ($P < 0.01$), 5 ($P < 0.05$), 6 ($P < 0.001$), and 8 ($P < 0.05$).

Means are shown in Fig. S3.

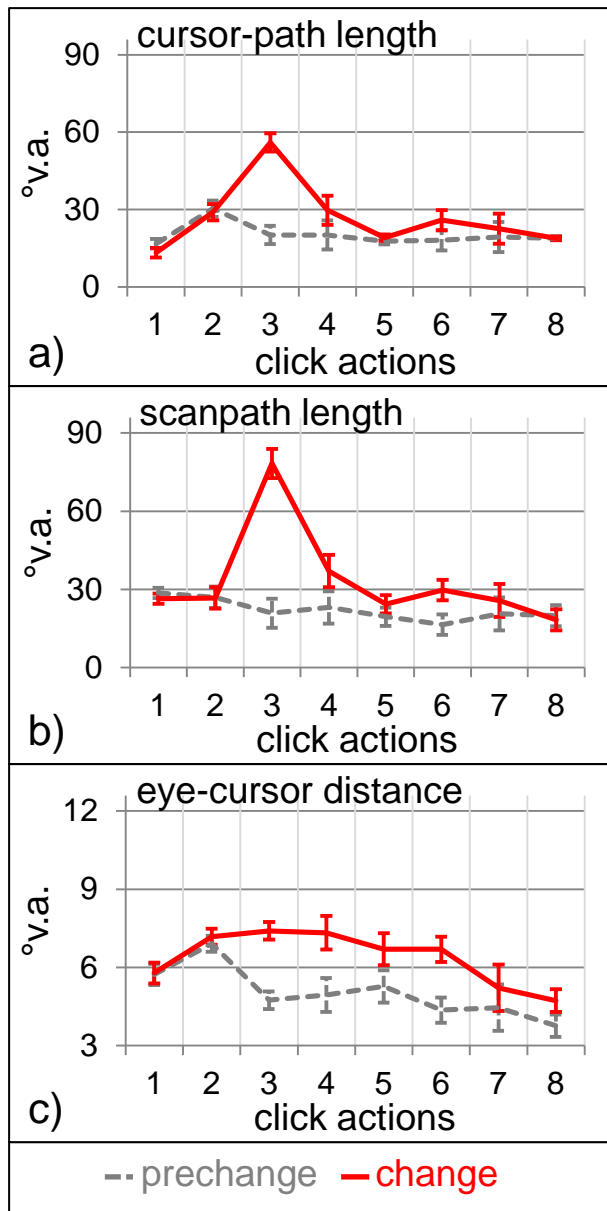


Figure S3. (a) Cursor-path length, (b) scanpath length, and (c) eye-cursor distance per phase (prechange, change) and click action (1-8). Error bars represent standard errors of the mean of the paired differences between prechange and change per click action.