Experimental Brain Research (2019) 237:1421–1430
https://doi.org/10.1007/s00221-019-05516-z

RESEARCH ARTICLE

Emergence of anticipatory actions in a novel task

Oliver Herbort[1] · Wilfried Kunde[1]

Received: 25 October 2018 / Accepted: 9 March 2019 / Published online: 19 March 2019

Abstract
Humans normally adapt earlier segments of multistep motor actions in such a way that the execution of later segments is facilitated. For example, the kinematics of grasping movements are adapted to the requirements of the intended subsequent object manipulations. Here we studied which factors foster adaptation of earlier action segments to later ones in a novel task for which no prior experience existed. Participants executed a two-step isometric force production task, in which the force produced in the first segment determined the difficulty of the second segment. Adaptation of the first segment to the second one benefited from explicit knowledge of the dependency between both segments but not from extensive prior experience with the second segment. These observations show that adaptation of motor actions to subsequent actions demands the construction of a task representation that allows to plan the first action segment with respect to its successor. How specifically the first segment is tailored to the second one does not depend on prior experience with the second segment but depends on experience from performing the interdependent two-step action sequence.

Keywords Motor control · Action planning · Anticipatory action · Action sequences · Isometric force

Introduction

Perceptual-motor skills usually involve the sequencing of actions. To facilitate the execution of critical or demanding actions in the sequence, the preceding actions are typically modified or additional, preparatory actions are inserted into the sequence. Thus, some effort is invested in earlier actions to support the execution of subsequent actions. Examples for this type of behavior can be found in highly skilled performance as well as mundane tasks: before high jump athletes take off, they perform a meticulously trained approach run. Before cyclists initiate a turn, they countersteer to lean into the curve. Before someone pulls a heavy door, the person leans away from the door to keep balance. And before a person manipulates an object, she adjusts the grasping movement to allow for a suitable grip. In the following, we refer to actions that are executed or modified to facilitate subsequent actions as anticipatory actions.

Although anticipatory actions have been documented in various domains (e.g., Cohen and Rosenbaum 2004; Cowie et al. 2010; Herbort 2012; Rosenbaum et al. 1990; Wing et al. 1997), it is unclear which factors foster their acquisition. The type of anticipatory actions that has received most scrutiny by far is grasp selection for object manipulation (for a review see Rosenbaum et al. 2012). The way objects are grasped typically depends on the subsequent manipulation of that object. For example, the arm is counterrotated while grasping to-be-rotated objects (e.g., Rosenbaum et al. 1990) and the position at which an object is grasped is inversely related to the intended direction of the object movement (e.g., Cohen and Rosenbaum 2004). Despite extensive research on this type of anticipatory actions, the question how anticipatory actions are acquired has rarely been addressed. However, two lines of research speak on that topic.

First, numerous studies have scrutinized the development of the ability to adjust one's grasp to intended object manipulations (for a review, see Wunsch et al. 2013). Albeit studies paint a mostly coherent picture of the development of this ability, which gradually levels up to a adult-like performance at the age of ten, they shed little light on the

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00221-019-05516-z) contains supplementary material, which is available to authorized users.

✉ Oliver Herbort
Oliver.Herbort@uni-wuerzburg.de

[1] Department of Psychology, University of Würzburg, Röntgenring 11, 97070 Würzburg, Germany

factors that enable adopting one's grasp to upcoming tasks. One exception is a study that tested whether social learning affects grip choice in 18- to 24-month olds, with a negative outcome, however (Jovanovic and Schwarzer 2011). Other studies reported a correlation between grasp selection for object manipulation and the ability to dissociate different types of visually presented grips or hands (Fuelscher et al. 2016; Stöckel et al. 2012; Toussaint et al. 2013). The results hint at the possibility that grasp planning is based on internal representations or motor imagery of the object manipulation action. As motor imagery requires some experience with a specific task (Rieger 2012), this account would suggest that experience with a task benefits the planning of respective anticipatory actions.

Second, in other experiments, participants grasped objects for slightly uncommon object manipulations (Mathews et al. 2017). Interestingly for the present question, post hoc analyses suggested that how participants represented the task-determined grasp selections. For example, some of Mathew et al.'s (2017) participants were asked to grasp a rotary control to rotate it 30° in one direction and then without releasing it 180° in the other direction. Apparently, some participants adopted the strategy of adjusting the grasp to the first 30° rotation step, whereas others started with that strategy but switched to making grasps contingent on the second 180° rotation step, which is arguably the more effective strategy for this task. Thus, participants reconfigured the task representation to select more effective grasps. Although these conclusions are based on post hoc analyses, they are in line with experiments showing that the framing of object manipulation tasks affects grasp selections (Herbort and Butz 2012; Herbort et al. 2014; Huhn et al. 2016). Moreover, they accord with the common notion that the development of perceptual-motor skills is initially under cognitive control (Fitts 1962, 1964; Willingham 1998).

In summary, many skills involve and benefit from anticipatory actions. However, how these actions are acquired in the context of a novel skill remains elusive. The introduction suggested two possible factors: experience with the task as a prerequisite for motor imagery-based planning and the construction of an adequate task representation. In the present article, we want to address whether these factors are involved in the acquisition of anticipatory actions in a task that is completely novel to participants. To tap into the first factor (i.e., experience), we either pre-trained participants with a task but without the possibility to use anticipatory actions (pre-training vs. no-pre-training). To elucidate the role of task representations, instructions either informed participants that the ease of executing the task could be influenced with an appropriate anticipatory action (informed) or provided no such information (naive). As we are interested in the acquisition of anticipatory actions, we are using an unfamiliar task. As will become apparent in the next section, the task has little overlap with common experimental or everyday tasks to prevent participants from transferring any implicit or explicit knowledge from such tasks to the present one.

Task

The task required participants to execute two successive actions, A1 and A2, in which rightly invested effort in A1 facilitated A2. During A1, participants produced an isometric force with a finger to either the left (denoted as negative force values) or right (positive values). During A2, participants then changed the isometric force produced at the end of A1 to move a cursor. How much the force had to be changed during A2, depended on the distance between the cursor and a target and was apparent to the participants from the outset. Importantly, the cursor movement in A2 corresponded to the change of the isometric force. For example, the force had to be changed by 10 N in A2, this could be achieved for example by terminating A1 with a force of 0 N and increasing the force to 10 N during A2, by terminating A1 with −5 N and increase the force to 5 N during A2, or by terminating A1 with −10 N and increasing the force to 0 N. In more general terms, participants could terminate A1 with an arbitrary force, which we henceforth term initial force, and then change the force by a prespecified value (target force change), requiring a total force of initial force + target force change at the end of A2. Thus, the force produced at the end of A1 set the baseline for A2 determining the isometric force at the end of A2.

In this task, initial forces that are inversely related to the force change required during A2—and thus allow ending A2 with a relatively low absolute force—are expected to minimize effort and maximize movement accuracy and speed. First, as participants typically spend a large proportion of the overall movement time precisely positioning the cursor in visually guided movements, such as A2, ending A2 with a low absolute force minimizes overall energy expenditure (Bolstad and Ersland 1978). Figure 1 confirms this assumption for the current experiment. Second, as the variability of isometric force increases with absolute force, low isometric force at the end of the movement (A2) allows for more precise and thus faster movements (Newell and Carlton 1988; Schmidt et al. 1979; Sosnoff and Newell 2005). Thus, if possible it was advantageous to devote a high portion of the overall required forces already to A1, to allow better control of A2. The result section will show that participants who adapted their A1 to A2 could execute A2 with less effort and within a shorter time. However, it is hard to predict a priori how participants trade off the investment of time and effort in A1 with the resulting payoffs in A2.

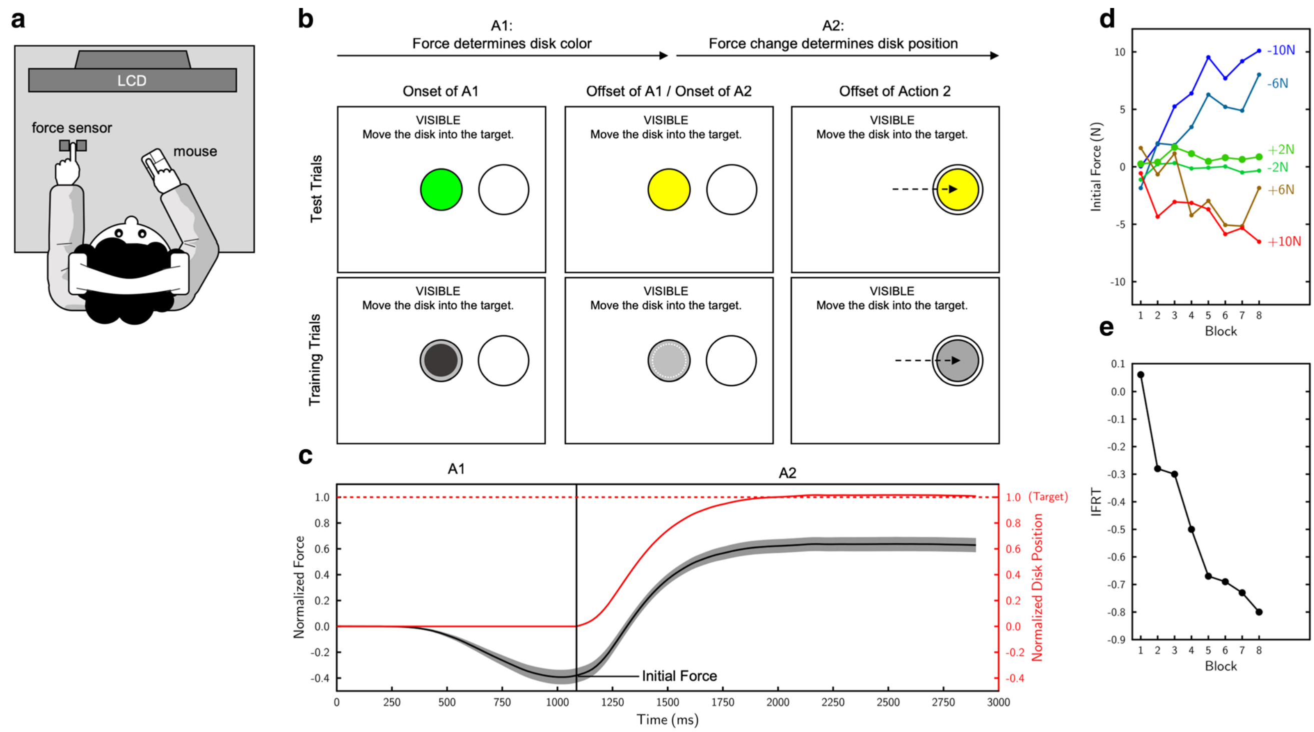

Fig. 1 Setup, procedure, and analysis. **a** The cartoon shows the experimental setup. **b** The figure illustrates the trial procedure in training and test trials, which consisted of two action steps. During A1, the force determined the disk color. Once the color was adjusted to the liking of the participant (test trials) or matched a prespecified target color (training trials), A2 started. During A2, changes in the force were displayed as movements of the disk. A2 ended, when the disk was positioned at the target (vision trials) or when participant clicked the mouse button (no-vision trials, not shown). **c** The chart shows the average time- and force-normalized trajectory of the isometric force (black) and the disk position (red) in vision trials of the last two test phase blocks. The variable "initial force" was extracted at the transition from A1 to A2. The shaded area shows one s.e.m. **d** The chart shows initial forces in trials with different target force changes (labels next to lines) of an exemplar participant. **e** The relationship between initial force and the target force change displayed in **d** is expressed in the variable IFRT (initial force relative to target) (Data from adapters and non-adapters, see "Results")

By design, our isometric force production task is relatively artificial and unrelated to common experimental or everyday tasks. What it shares with other tasks is that the ease or performance of action execution (here of A2) depends on the initial body state (initial force), which can be adjusted a priori by an anticipatory action (A1). As outlined in the introduction, this underlying principle applies to action in almost all domains. For example, soccer players may run a curved path to a ball to approach it from an angle that facilitates passing to a teammate. Before we use tools, we adjust the grip to the planned tool use action. And when someone wants to drag files over the desktop using the computer mouse, the person may reposition the mouse on the mouse pad beforehand.

Hypotheses

Previous observations suggest (Mathew et al. 2017) that not all participants make use of anticipatory actions (i.e., produce initial forces that are inversely related to the target force of A2). Therefore, we were prepared to encounter a similar separation in two groups (adapters and non-adapters) here as well. Moreover, we expect that participants who do show anticipatory actions, produce different anticipatory actions in earlier blocks depending on their task representations and prior experience with A2 but then converge toward a common, a priori unknown optimum.

With respect to the factors that govern this adaptation, we had two hypotheses. According to the experience hypothesis, the planning of A1 rests on imagery of A2. Adaptation of A1 to A2 should be facilitated when participant can acquire an internal representation of A2 during a pre-training phase, even when pre-training does not yet allow to adapt A1 to A2. The hypothesis would be supported if participants who received pre-training blocks with A2 are more likely to adapt A1 to A2 and do so more strongly during early test blocks. If that is not the case, planning A1 with respect to A2 could be considered a subskill that develops independently of the ability to control A2 (cf. Herbort et al. 2018).

According to the task representation hypothesis, anticipatory actions hinge on the construction of a task representation that allows making A1 contingent on the requirements of A2. Participants who are explicitly informed about this possibility should be more likely to construct such a task representation. They should thus be more likely to use anticipatory actions and adapt A1 to A2 more strongly during early test blocks than naïve participants. If this is not the case, it would suggest that the construction of an adequate task representation is not critical, for example, because actions are adapted to their successors by default.

Finally, to test to which extent the information about A2 acquired during pre-training may be used to plan A1, we introduced two additional control conditions. First, we used a third instruction which informed participants not only that the initial force may facilitate A2 but asked them to produce initial forces that allowed to end A2 with exactly zero force (instructed). We included this condition to test whether participants can use the information acquired during pre-training when A1 is planned in a more deliberate, explicit way. Second, to check whether participants acquire information during pre-training that go beyond the online control of the cursor (i.e., information that could be used for motor imagery-based planning), we included trials in which A2 had to be feedforward controlled. The cursor was not visible in these trials and had thus been controlled based on internal models. Finally, we tested how anticipatory actions affected effort, speed, and accuracy of A2.

Method

Participants

120 right-handed participants (94 females, 26 males, age $M = 26.3$, $SD = 7.1$)[1] were recruited for the experiment. They signed informed consent and received 6 € or course credit for their participation. The experiment was in accordance with the institutional ethical standards and with the 1964 Helsinki Declaration and its later amendments.

Stimulus and apparatus

Participants were seated at a table, on which a force sensor, a computer mouse, and an LCD Monitor (17″, 1280 × 1024 pixel) were placed (Fig. 1a). The custom build force sensor consisted of two elements, which allowed to record isometric force production to the left and to the right. The distance between the two elements was adjustable and fitted to the width of the participant's index finger.

The task was presented on the LCD against a black background. The cursor disk (diameter 14 mm) was initially presented in the center of the screen. A target circle (diameter 17 mm) was horizontally displaced from the center of the screen according to the target force change that was required during A2 (1 N corresponded to 5 mm). During A1, the force at the sensor determined the cursor's color. In test blocks, participants could select an arbitrary color (and thus initial force) from a blue–green–yellow gradient. More specifically, the disk was blue when the force was − 12 N or less (12 N or more), the disk was green when no force was applied, and the disk was yellow when the force was 12 N or more (− 12 N or less). Intermediate forces were represented by intermediate colors. In the pre-training blocks, the color was picked from a white-to-dark gray gradient in likewise fashion. In this condition, the force determined the luminosity of the inner part of the disk (diameter 10 mm). The surrounding ring had a color that could be matched by exerting a specific initial force. The mapping between colors and force was counterbalanced over participants. The coloring task was introduced to help participants control the initial force in test trials and to obscure the relationship between A1 and A2.

Procedure

Participants sat at the table, rested the left forearm on the table surface and put the left index finger into the force sensor (Fig. 1a). Participants were instructed to use the wrist and index finger to produce isometric forces. They held a computer mouse with the right hand and wore headphones.

Figure 1b shows the events in training and test trials. An animation of the trial procedure is provided as electronic supplement. A1 began with the presentation of the cursor disk and the target circle. Additionally, a short instruction at the top of the screen informed whether the trial was a vision trial or no-vision trial (German translations of: "VISIBLE: move the disk into the target" printed in green or "INVISIBLE: move the invisible disk into the target. Then press the mouse button." printed in cyan). In test blocks, participants were free to produce any initial force (and thus disk color) and A1 was considered finished when participants pressed the left mouse button with the right index finger. In the training blocks, participants were instructed to match the color of the disk to that of the surrounding ring, thus producing a predetermined initial force. Under this condition, A1 was considered finished when the isometric force was within 1 N of the predetermined initial force for 200 ms. A short beep was played (880 Hz, 50 ms) at the end of A1. From this moment on, the color of the cursor disk did not change anymore.

A2 directly followed A1. The cursor disk could now be moved to the left and right by changing the force. The position of the cursor disk relative to the screen's center was determined by the difference between the current isometric force and the initial force (1 N corresponded to 5 mm). That

[1] 18 participants did not disclose their age or it was not registered.

is, a reduction of left-ward force or an increase of right-ward force moved the disk to the right, while a reduction of right-ward force or an increase of left-ward force moved the disk to the left. Figure 1c shows the normalized force and cursor position in A1 and A2.

In vision trials, the cursor disk stayed visible. The target was considered hit when the center of the cursor disk stayed within 5 mm (1N) of the center of the target circle for 1000 ms. In no-vision trials, the cursor disk disappeared once it has been moved more than 2.5 mm from its initial position. Participants clicked the mouse button, once they thought they correctly positioned the cursor disk. After that, the cursor disk appeared at the final position for 500 ms. After A2, the German translation of "well done!" was displayed for 1000 ms, except when participants missed the target by more than 1 cm (2 N) in no-vision trials, in which the text red "Miss!".

The pre-training group worked through eight training blocks followed by eight test blocks. In the training blocks, half of the participants were required to produce initial forces of − 4 N (by matching the color of disk and ring) and the other half initial forces of 4 N. These initial forces were selected to allow participants to experience that the force change controls the cursor position. The no-pre-training group received a total of 16 test blocks. The first eight test blocks were collected for comparison with the test blocks of the pre-training group. The remaining test blocks were included, because we wanted to schedule equally long sessions for each condition and to check whether initial forces were further adapted after the end of the eight test blocks.

Each block consisted of four repetitions of vision trials and one no-vision trial for each of the target force changes of − 10 N, − 6 N, − 2 N, 2 N, 6 N, and 10 N. Six warm-up trials, in which participants only executed A1 with different fixed initial forces (− 10 N, − 6 N, − 2 N, 2 N, 6 N, 10 N) were administered before the 1st and 9th block. In total, each participant performed 492 trials in a 30 min session.

Participants were split randomly into six groups, defined by the factors instruction (naïve, informed, instructed) and training (pre-training vs. no-pre-training). Twenty-four participants were assigned to each of the naïve and informed groups. Only twelve participants were collected for each of the instructed group, because we expected that all participants adapt the initial force to the target—unlike in the other groups. Before pre-training blocks, participants were instructed to first match the color of the ring to the color of the disk and then move the disk to the target in all instruction conditions. Before test blocks, participants received group-specific instructions. In the naive conditions, participants were informed that they could first adjust the color of the disk to their liking and then had to move the disk into the target. In the informed conditions, participants were explicitly informed that they could reduce the force required to hit the target by exerting an initial force in the other direction. However, no instructions were given to trade-off initial force for final force or how that trade-off should be balanced. In the instructed conditions, participants were instructed as in the informed conditions but were additionally asked to select an initial force that allowed them to position the cursor disk with as little final force as possible.

Data reduction and analysis

The main dependent variable was the relationship between the target force change and the initial force, which was the force produced at the end of A1 (Fig. 1c, d). This relationship was quantified by the slope of the linear regression of initial force on the target force change in vision trials for each block and participant (Fig. 1e). We refer to the slope as initial force relative to target (IFRT). IFRT was zero when participants did not adjust the initial force to the target force. When IFRT assumed a value of − 1, participants produced an initial force that allows them to hit the target of A2 with constant (ideally zero) force. Figure 1d shows the evolution of the relationship between initial forces and target force change over eight test blocks for an exemplar participant. Figure 1e shows the resulting IFRT values. The absolute error was the mean absolute deviation of the disk position from the target position at the end of A2 of no-vision trials (expressed in N). The effort was defined as the integral of the absolute force over the duration of A1 and A2. Movement time 1 was defined as the interval from stimulus onset to the end of A1. Movement time 2 was defined as the interval between the offset of A1 and the offset of A2. Warm-up trials and trials in which movement time 1 or movement time 2 exceeded 10 s were excluded from the analysis (0.68% of trials).

Results

Frequency of anticipatory actions

Figure 2a shows the mean IFRTs in the 7th and 8th test block ($IFRT_{78}$). The histogram clearly reveals that participants fell into two groups. The adapters produced an initial force in A1 that was inversely related to the target force change, as indicated by negative IFRT values. These participants showed anticipatory actions. For non-adapters, the initial force was unrelated to the target force change and they thus did not exhibit anticipatory actions. Participants were classified based on the histogram in Fig. 2a. Participants were considered adapters if their mean $IFRT_{78}$ was lower than − 0.2 (57.5%), were considered non-adapters when the $IFRT_{78}$ was between − 0.2 and 0.2 (40.8%). The classification criterion was determined post hoc based on the

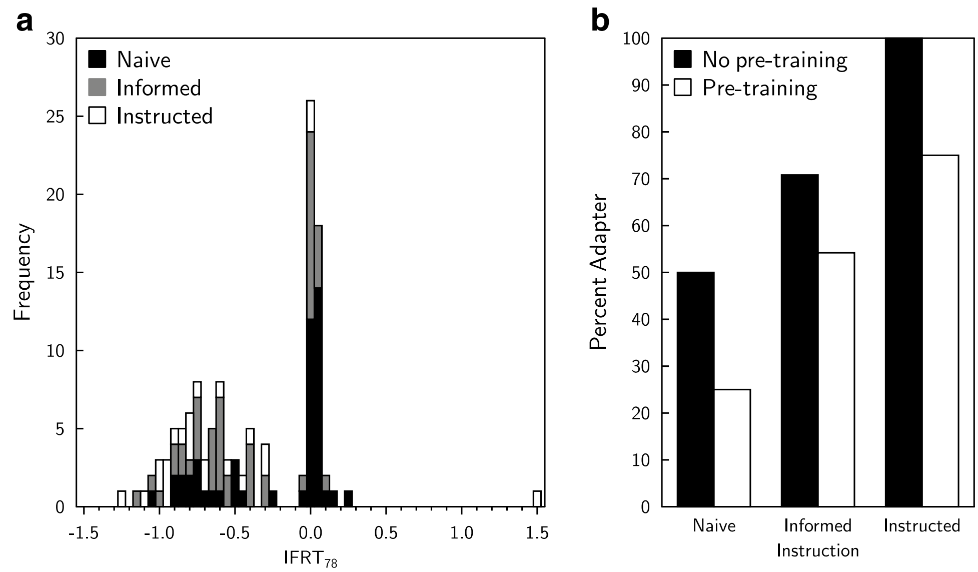

Fig. 2 Adaptation of initial force **a** Histogram of $IFRT_{78}$. **b** Percentage of participants adapting their initial force to the target force in blocks 7 and 8 of the test phase

histogram but is justified by the clear bimodal distribution in Fig. 2a. The criterion was further validated by an analysis of the within-block and within-participant correlations between initial force and target force change: all adapters but none of the non-adapters revealed a significant negative correlation in the 7th or 8th test block ($\alpha = 0.05$). The IFRT of two participants (1.7%) exceeded 0.2. These participants can be considered "anti-adapters", because they select IFRTs that increase the required final force. Due to the low number of cases and the unclear theoretical implications of this type of behavior, the anti-adapters were excluded from further analysis. Subsuming anti-adapters into the class of non-adapters would not have changed the outcomes statistical tests.

Two-sided Fisher's exact tests revealed the following effects of pre-training and instruction on the frequency of adapter types (we report unadjusted and Bonferroni–Holm corrected p values). Pre-trained participants were less frequently classified as adapters than untrained participants, $p = 0.039$ ($p_{adjusted} = 0.039$). Informed participants were more frequently adapters than naïve participants, $p = 0.024$ ($p_{adjusted} = 0.048$) and less frequently adapters than instructed participants, $p = 0.012$ ($p_{adjusted} = 0.036$). Thus, explicit instructions increased the probability that a participant adapted the initial force to the target force change, as predicted by the task representation hypothesis. Pre-training without the ability to adapt the initial force even decreases the likelihood of adapting initial forces once this became possible.

Adapter's IFRTs in the test phase

Next, we tested whether instruction and pre-training affected the IFRTs of adapters in the first two test blocks. For statistical analysis, the mean IFRTs of the first two blocks ($IFRT_{12}$) were submitted to an ANOVA with between-participant factors of training and instruction. The instruction affected $IFRT_{12}$s, $F(2,63) = 8.73$, $p < 0.001$, $\eta^2_p = 0.22$. There was no main effect of training, $F(1,63) = 1.41$, $p = 0.240$, $\eta^2_p = 0.02$. Both factors interacted, $F(2,63) = 4.50$, $p = 0.015$, $\eta^2_p = 0.13$. A follow-up ANOVA that included the factor training and the factor instruction with the levels naive vs. informed revealed lower $IFRT_{12}$s in the naive conditions than in the informed conditions, $F(1,44) = 8.41$, $p = 0.006$, $\eta^2_p = 0.16$, no main effect of training, $F(1,44) = 0.05$, $p = 0.825$, $\eta^2_p = 0.00$, and no interaction, $F(1,44) = 3.42$, $p = 0.071$, $\eta^2_p = 0.07$. A similar ANOVA comparing the informed conditions with the instructed conditions revealed no effect of instruction, $F(1,47) = 2.80$, $p = 0.101$, $\eta^2_p = 0.06$, no effect of training, $F(1,47) = 0.46$, $p = 0.501$, $\eta^2_p = 0.01$, and a significant interaction, $F(1,47) = 7.63$, $p = 0.008$, $\eta^2_p = 0.14$. T tests conducted for each instruction condition revealed no significant effects of training in naive condition, $t(16) = 1.19$, $p = 0.252$, $d_s = 0.56$, and in the informed condition, $t(28) = -1.62$, $p = 0.116$, $d_s = 0.60$. Training affected $IFRT_{12}$ in the instructed condition, $t(19) = 2.25$, $p = 0.037$, $d_s = 0.99$.

Figure 3 also shows that all groups converged toward an IFRT of about −0.7 at the end of the test block. Accordingly, an ANOVA on the IFRT in the last two subblocks ($IFRT_{78}$) revealed no effects of training, $F(1,63) = 0.02$, $p = 0.888$, $\eta^2_p = 0.00$, no effects of the instruction, $F(2,63) = 1.57$, $p = 0.216$, $\eta^2_p = 0.05$, and no interaction, $F(2,63) = 0.99$, $p = 0.376$, $\eta^2_p = 0.03$. Finally, participants in the no-pre-training group continued with a second test phase, in which IFRTs remained by and large at the level observed at the end of the (first) test phase ($IFRT_{78}$ vs. mean IFRT of the second test phase: naïve −0.70 vs. −0.78; informed: −0.70 vs. −0.75; instructed: −0.72 vs −0.71). This suggests that

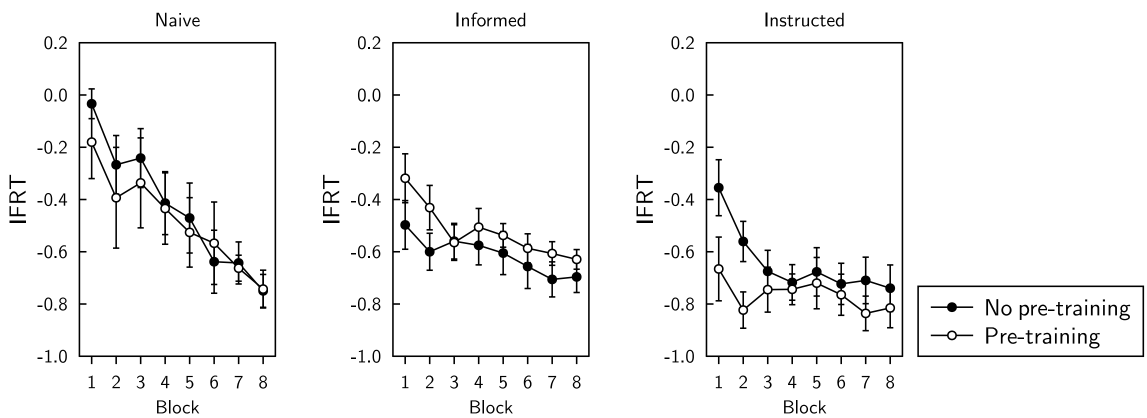

Fig. 3 Adapter's IFRT in the test phase by instruction and training condition. Error bars show s.e.m

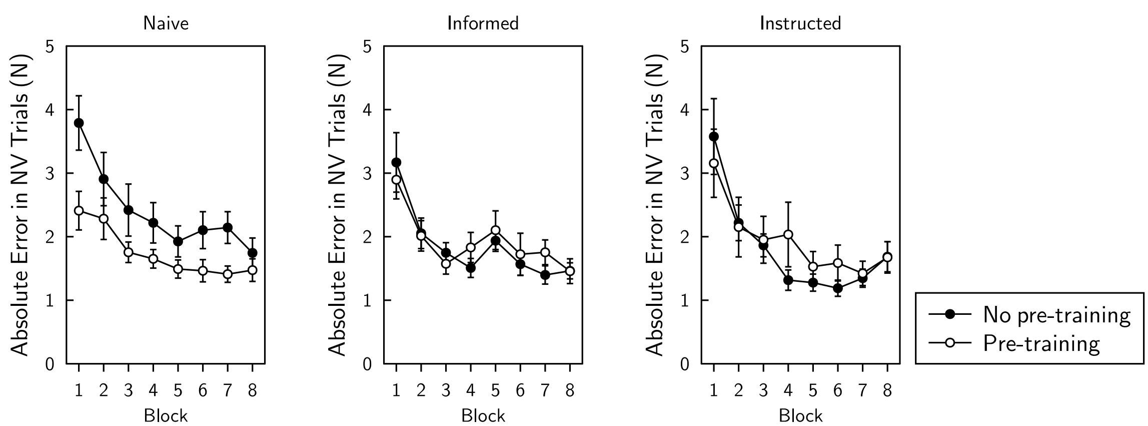

Fig. 4 Absolute errors in no-vision trials in the test phase by instruction and training condition. Error bars show s.e.m

participants converged toward a common IFRT by the 8th test block.

Absolute errors in no-vision trials

Next, we tested whether groups differed with respect to their ability to control the cursor without vision in the first two blocks (Fig. 4). The absolute errors of adapters and non-adapters in the no-vision trials were subjected to an ANOVA with factors of instruction and training. The instruction had no significant effect, $F(2,112) = 0.54$, $p = 0.584$, $\eta^2_p = 0.01$. Training had no significant effect, $F(1,112) = 2.49$, $p = 0.117$, $\eta^2_p = 0.02$. Likewise, the interaction was not significant, $F(2,112) = 1.03$, $p = 0.360$, $\eta^2_p = 0.02$.

Effects of anticipatory actions

Finally, we compared the average performance of adapters and non-adapters in the last two subblocks of the test phase. Figure 5a shows that the absolute errors of both groups in the no-vision trials were almost identical, $t(116) = -0.01$, $p = 0.991$, $d_s = 0.00$.

Figure 5b shows the average effort put into A1 and A2. A split-plot ANOVA with a between-participant factor of adapter type (adapter vs. non-adapter) and a within-participant factor of action (A1 vs. A2) revealed the following effects.[2] The effort of adapters was lower than that of non-adapters, $F(1,110) = 20.85$, $p < 0.001$, $\eta^2_p = 0.16$. Less effort was put in Action 1 than in Action 2, $F(1,110) = 358.47$, $p < 0.001$, $\eta^2_p = 0.77$. Both factors interacted, $F(1,110) = 186.69$, $p < 0.001$, $\eta^2_p = 0.63$. Non-adapters put less effort in A1 than adapters, $t(110) = 6.74$, $p < 0.001$, $d_s = 0.643$. The reverse pattern was found for A2, $t(62.37) = 8.39$, $p < 0.001$, $d_s = 1.80$.

A similar ANOVA was conducted for the movement times in the last two blocks of the test phase. Adapters moved slower than non-adapters, $F(1,116) = 40.88$, $p < 0.001$,

[2] Six participants were excluded from this analysis because the effort has not been correctly registered during the experiment.

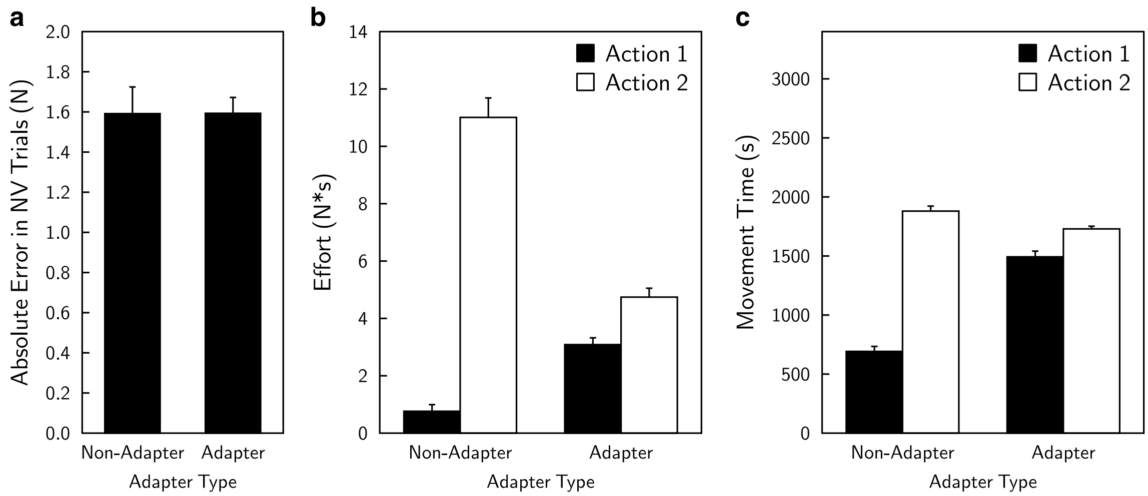

Fig. 5 Effects of adapting the initial force. Absolute errors (**a**), effort of Action 1 and Action 2 (**b**), and movement time of Action 1 and Action 2 by adapter type. Error bars show s.e.m

$\eta^2_p = 0.26$. A1 was shorter than A2, $F(1,116) = 570.86$, $p < 0.001$, $\eta^2_p = 0.83$. Both factors interacted, $F(1,116) = 229.24$, $p < 0.001$, $\eta^2_p = 0.66$. A1 was shorter for non-adapters than for adapters, $t(115.82) = 12.01$, $p < 0.001$, $d_s = 2.13$. Inversely, A2 was shorter for the adapters than for non-adapters, $t(75.53) = 3.15$, $p = 0.002$, $d_s = 0.63$.

Discussion

The present experiment addressed two hypotheses. The experience hypothesis stated that prior experience with a task (A2) enhances the acquisition of anticipatory actions (A1). This hypothesis was not supported by the data. In fact, participants who practiced a task without the possibility for anticipatory actions were less likely to use anticipatory actions once this became possible than participants who had no prior experience at all. Moreover, anticipatory actions of those participants who ultimately used them were not significantly affected by prior experience. An exception was the condition in which participants were explicitly instructed to use anticipatory actions. Here, only prior experience allowed participants to readily implement the instruction.

Second, we addressed whether an appropriate task representation needs to be developed to implement anticipatory actions in the context of a novel skill. This hypothesis was confirmed. Participants who were informed about the dependency between both action segments were more likely to use anticipatory actions. Moreover, informed participants adapted their anticipatory actions stronger to the task requirements in the early test blocks than naïve participants. This suggests that it is necessary to construct a task representation that allows to plan an action contingent on its successor and that subsequent actions are not considered by default when planning action sequences. A comparison of adapters and non-adapters revealed that anticipatory actions reduced the overall effort of the task but was accompanied with an increase in overall movement duration. An open question is whether the reconfiguration of the task representation or the execution of anticipatory actions is necessarily an explicit process. In the present experiment, participants were mostly aware of the used strategies by the end of the experiment. In a post-experiment questionnaire, 67% of adapters indicated that they adapted the initial force of A1 to A2, 25% of them said they changed the initial force, and only 8% noted that they used constant initial forces. The pattern was reversed for non-adapters who mostly stated that they used constant initial forces (89%) and rarely indicated that they changed the initial force (9%) or adapted it to A2 (2%). However, we doubt that such explicit processes are necessary to acquire anticipatory actions. At least, anecdotal experience from our lab suggests that participants are not always aware of their anticipatory actions.

A surprising finding was that training the task without the possibility for anticipatory actions reduced the likelihood that participants would use anticipatory actions once this became possible. One possible explanation for this effect is that pre-training made participants more effective in carrying out A2 without adapting A1. However, this was not borne out by the data. Both trained and untrained adapters had to invest less total effort in the task than non-adapters. The advantage of adapting for trained participants (adapter: 6.7 Ns vs. non-adapter: 12.5 Ns) was even greater than for untrained participants (adapter: 8.6 Ns vs. non-adapter: 10.5 Ns). This suggests that it may be difficult to switch to a look-ahead planning strategy, which considers the demands of upcoming actions, when such a strategy has not been employed previously. It seems as if extended practice with a task blinded participant to adjust task execution to constraints imposed by a subsequent task.

An interesting dissociation has been found between the early anticipatory actions of the informed and instructed groups. The instructed participants could use their pre-training experience to plan anticipatory action in such a way that a specific outcome was by and large obtained (i.e., minimal force at the end of A2), whereas merely informed participants did not benefit from pre-training. Apparently, the presumably more explicit mode of action planning in the instructed condition allowed participants to transfer information from the hitherto relatively unrelated task A2, whereas this was not possible in the more implicit mode of control used in the other conditions.

The current experiment likewise shows that acquired internal representations, such as the mapping from cursor movements to force changes in the present task, are not involved in anticipatory action planning when participants are naïve or only informed about the dependency of A2 on A1. Likewise, expectable but yet unexperienced requirements of object manipulations typically had little or no effects on grasp selections in other studies (Herbort et al. 2017, 2018). These findings suggest that participants use an implicit, experience-based mode of action planning by default. Only when they explicitly aimed to adapt A1 to A2 in a specific way in the instructed condition, participants planned A1 based on an internal representation of A2, as implied by the motor imagery account.

Finally, the study has implications for the understanding of anticipatory actions and its development. First, the results indicate that the display of anticipatory actions depends on several factors. In the present experiment alone, at least three factors were involved. First, anticipatory actions have to be beneficial. In our experiment, anticipatory actions reduced overall effort. In other tasks, anticipatory action increase movement efficiency (Short and Cauraugh 1999) or extent the range of possible actions. Second, a suitable task representation is necessary. In our experiment, the task representation was manipulated by explicit instructions. However, several naïve participants also displayed anticipatory actions. Previous experiments suggest that the experience of movement inefficiency may trigger the updating of the task representation (Mathew et al. 2017). Finally, after reconfiguration of the task representation, further experience allows to fine tune anticipatory action to the specific requirements of the task and the involved movements (cf. Herbort et al. 2014, 2017). In conclusion, the display of anticipatory actions or "second order planning" (Rosenbaum et al. 2012) is not a unitary capacity but the result of a specific combination of individual experiences, task conditions, and various cognitive processes. This view might also explain the weak correlations between anticipatory actions in different tasks and differences in the developmental trajectories (Wunsch et al. 2016).

In summary, the present paper shows that prior experience with a task does not necessarily benefit the development of anticipatory actions. It seems crucial to develop a task representation that allows to make the actions that lead up to a more critical action, such as the approach run before a jump or the grasp before an object manipulation, contingent on the later action. How such task representations are spontaneously developed is still an open question. Answering that question, however, may be an important step for understanding how we acquired the different types of anticipatory actions, which make our life easier every day.

Acknowledgements We thank Georg Schüssler and Albrecht Sebald for technical support and Lorena Fleischmann for preparing and running the experiment.

References

Bolstad G, Ersland A (1978) Energy metabolism in different human skeletal muscles during voluntary isometric contractions. Eur J Appl Physiol Occup Physiol 38:171–179. https://doi.org/10.1007/BF00430075

Cohen RG, Rosenbaum DA (2004) Where grasps are made reveals how grasps are planned: generation and recall of motor plans. Exp Brain Res 157:486–495. https://doi.org/10.1007/s00221-004-1862-9

Cowie D, Smith L, Braddick O (2010) The development of locomotor planning for end-state comfort. Perception 39(5):661–670. https://doi.org/10.1068/p6343

Fitts PM (1962) Factors in complex skill training. In: Glaser R (ed) Training research and education. University of Pittsburgh Press, Pittsburgh, pp 177–197

Fitts PM (1964) Perceptual-motor skill learning. In: Melton AW (ed) Categories of human learning. Academic Press, Oxford, pp 243–285

Fuelscher I, Williams J, Wilmut K, Enticott PG, Hyde C (2016) Modeling the maturation of grip selection planning and action representation: insights from typical and atypical motor development. Front Psychol 7:108. https://doi.org/10.3389/fpsyg.2016.00108

Herbort O (2012) Where to grasp a tool? Task-dependent adjustments of tool transformations by tool users. Z Psychol 220:37–43. https://doi.org/10.1027/2151-2604/a000089

Herbort O, Butz MV (2012) The continuous end-state comfort effect: weighted integration of multiple biases. Psychol Res 76:345–363. https://doi.org/10.1007/s00426-011-0334-7

Herbort O, Butz MV, Kunde W (2014) The contribution of cognitive, kinematic, and dynamic factors to anticipatory grasp selection. Exp Brain Res 232:1677–1688. https://doi.org/10.1007/s00221-014-3849-5

Herbort O, Mathew H, Kunde W (2017) Habit outweighs planning in grasp selection for object manipulation. Cogn Psychol 92:127–140. https://doi.org/10.1016/j.cogpsych.2016.11.008

Herbort O, Kirsch W, Kunde W (2018) Grasp planning for object manipulation without simulation of the object manipulation action. J Exp Psychol 45(2):237–254

Huhn JM, Potts CA, Rosenbaum DA (2016) Cognitive framing in action. Cognition 151:42–51. https://doi.org/10.1016/j.cognition.2016.02.015

Jovanovic B, Schwarzer G (2011) Learning to grasp efficiently: the development of motor planning and the role of observational learning. Vis Res 51:945–954. https://doi.org/10.1016/j.visres.2010.12.00

Mathew H, Kunde W, Herbort O (2017) Inverting the planning gradient: adjustment of grasps to late segments of multi-step object manipulations. Exp Brain Res 235:1397–1409. https://doi.org/10.1007/s00221-017-4892-9

Newell KM, Carlton LG (1988) Force variability in isometric responses. J Exp Psychol Hum Percept Perform 14:37–44. https://doi.org/10.1037/0096-1523.14.1.37

Rieger M (2012) Motor imagery in typing: effects of typing style and action familiarity. Psychonom Bull Rev 19:101–107. https://doi.org/10.3758/s13423-011-0178-6

Rosenbaum DA, Marchak F, Barnes HJ, Vaughan J, Slotta JD, Jorgensen MJ (1990) Constraints for action selection: overhand versus underhand grips. In: Jeannerod M (ed) Attention and performance, vol XIII. Lawrence Erlbaum Associates, Hillsdale, pp 321–345

Rosenbaum DA, Chapman KM, Weigelt M, Weiss DJ, van der Wel R (2012) Cognition, action, and object manipulations. Psychol Null 138:924–946. https://doi.org/10.1037/a0027839

Schmidt RA, Zelaznik H, Hawkins B, Frank JS, Quinn JT (1979) Motor-output variability: a theory for the accuracy of rapid motor acts. Psychol Rev 86:415–451. https://doi.org/10.1037/0033-295X.86.5.415

Short MW, Cauraugh JH (1999) Precision hypothesis and the end-state comfort effect. Acta Psychol 100(3):243–252. https://doi.org/10.1016/S0001-6918(98)00020-1

Sosnoff JJ, Newell KM (2005) Intermittent visual information and the multiple time scales of visual motor control of continuous isometric force production. Perc Psychophys 67:335–344. https://doi.org/10.3758/BF03206496

Stöckel T, Hughes CML, Schack T (2012) Representation of postures and anticipatory motor planning in children. Psychol Res 76:768–776. https://doi.org/10.1007/s00426-011-0387-7

Toussaint L, Tahej P-K, Thibaut J-P, Possamai C-A, Badets A (2013) On the link between action planning and motor imagery: a developmental study. Exp Brain Res 231:331–339. https://doi.org/10.1007/s00221-013-3698-7

Willingham DB (1998) A neuropsychological theory of motor skill learning. Psychol Rev 105:558–584. https://doi.org/10.1037/0033-295X.105.3.558

Wing AM, Flanagan JR, Richardson J (1997) Anticipatory postural adjustments in stance and grip. Exp Brain Res 116:122–130. https://doi.org/10.1007/PL00005732

Wunsch K, Henning A, Aschersleben G, Weigelt M (2013) A systematic review of the end-state comfort effect in normally developing children and in children with developmental disorders. J Motor Learn Develop 1:59–76. https://doi.org/10.1123/jmld.1.3.59

Wunsch K, Pfister R, Henning A, Aschersleben G, Weigelt M (2016) No interrelation of motor planning and executive functions across young ages. Front Psychol 7:1031. https://doi.org/10.3389/fpsyg.2016.01031