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Precise Movements in Awkward Postures:

A Direct Test of the Precision Hypothesis of the End-state Comfort Effect

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Author note

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The data are available online (https://osf.io/3jcb4/).

Abstract

When humans manipulate an object, they prefer to grasp the object in a way that allows to terminate the manipulation in a comfortable posture. The reasons for this end-state comfort effect have remained elusive so far. One explanation assumes that comfortable end-states are not preferred per se, but rather because they come with increased movement precision, which is typically required by the end of an object manipulation. Five experiments were conducted to test this hypothesis and yielded three main results. First grasps that increase control over an object are preferred irrespective of the resulting arm postures. Second, differences in the controllability associated with comfortable and uncomfortable postures are sufficient to elicit the end-state comfort effect. Third, grasps that optimize control are preferred even when this implies adopting uncomfortable end-states. Altogether, these findings directly support the hypothesis that the end-state comfort emerges because it maximizes the control over the manipulated object at the end of object manipulations.

Keywords

grasp planning; object manipulation; end-state comfort effect; virtual reality; motor control

Public Significance Statement

Our movements typically reflect immediate but also later action goals. This anticipatory aspect of human action also becomes apparent when we adapt our grasping movements to the subsequent manipulations of the grasped objects. We show that grasp selections maximize the speed and accuracy of object manipulations.

Precise movements in awkward postures: A direct test of the precision hypothesis of the end-state comfort effect

When we grasp objects in order to manipulate them, we typically select grasps that facilitate the planned object manipulation. An example is the rotation of an over-turned glass. Most people would twist their arm before grasping the glass so that the base of the thumb points downward. During the rotation, the arm would then unwind into a more comfortable arm posture (i.e., a posture in the middle of the arm's range of motion) which allows to put the glass gently on a table. By contrast, a comfortable grasp would be selected almost certainly for moving the glass elsewhere without rotating it. This phenomenon has been termed "end-state comfort effect" (Rosenbaum & Jorgensen, 1992; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992). Subsequent research has shown that the planned interaction with an object is a key determinant of grasp selection in many object manipulation tasks (for a review see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012).

But why exactly are some grasps preferred over others? Rosenbaum and colleagues (1990) initially suggested that participants grasp objects awkwardly for rotations because this builds up elastic energy in the arm muscles. The elastic energy is then released when the arm unwinds into a comfortable posture, thus facilitating the object rotation (Rosenbaum et al., 1990). Later on, it has been reasoned that grasp selections maximize the control over the object, thus enabling more precise and faster object manipulations (Künzel et al., 2013; Rosenbaum, van Heugthen & Caldwell, 1996; Rosenbaum, Vaughan, Jorgensen, Barnes & Stewart, 1993; Rosenbaum et al., 2012; Short & Cauraugh, 1999). As objects can be handled more precisely with a comfortable posture and as it is usually most important to have a high level of control at the end of the object manipulation, it follows that participants favor grasps that result in a comfortable posture at the end of the object manipulation (end-state). This hypothesis has been called the "precision hypothesis" (Rosenbaum et al., 1993, 1996).

Evidence for the precision hypothesis

Two lines of evidence support the precision hypothesis. The first line of evidence pertains to a precondition of the precision hypothesis, namely that comfortable postures maximize the control over an object. Rosenbaum et al. (1996) tested this hypothesis by asking participants to oscillate a dowel with either comfortable or uncomfortable arm postures. They found that oscillations reached the highest frequency in the comfortable postures. Likewise, Potts, Brown, Solnik, & Rosenbaum (2017) showed that participants could hold a dowel more steadily in comfortable than in uncomfortable postures.

Other studies examined the effect of different grips on the speed and precision of entire object manipulations. In one example, participants had to grab a bar and stamp targets on a wall with it (Short & Cauraugh, 1999). Participants were instructed to use different grips which resulted in either a comfortable or uncomfortable posture when hitting the target. Participants were about four times more accurate when they hit the target in a comfortable posture. However, more nuanced observations have been reported in other studies. In one study participants had to move and rotate a cylinder to different final positions via an intermediate position (Seegelke, Hughes, Knoblauch, & Schack, 2015). The participants who terminated the object manipulation in the most comfortable postures also positioned the cylinder more accurately, but only in two out of the four tested object manipulations. In another experiment, participants were instructed to use various grips for the rotation of a knob (Herbort, 2015). In this task, the fastest rotations began with a neutral, comfortable grip and ended in a more excursed, uncomfortable posture.

In summary, several experiments showed that participants can manipulate objects more accurately or faster when they wield them in comfortable postures, although other experiments revealed only partial or no benefits of the end-state comfort effect. This line of evidence thus supports a crucial precondition of the precision hypothesis. However, it does not directly pertain to the factors that determine grasp selection: Although comfortable end-states facilitate control, they may be adopted for other reasons, such as simply comfort, the exploitation of elastic energy, or the leeway they offer for further object manipulations.

The second line of evidence in support of the precision hypothesis shows that grasp selections are affected by the control requirements associated with the initial and final phase of an object manipulation. In a representative study, participants had to manipulate a bar that was attached to a large disk (reminiscent of the lid of a pan, Künzell et al., 2013). The object was initially positioned behind a screen with two circular openings. It had to be fetched from behind the first opening, rotated by 180° and moved up-side down through a second opening. Participants preferred initial uncomfortable grips more when they had to clear a large opening first and a small opening second than with a small opening first, and a large opening second. Thus, the more important it was to have precise control over the object at the end of the object manipulation, the more pronounced was the end-state comfort effect. Comparable modulations of the end-state comfort effect have been reported in other studies (Hughes, Seegelke, & Schack, 2012; Rosenbaum et al., 1996; Stöckel & Hughes, 2015; cf. Short & Cauraugh, 1999; for an exception see Rosenbaum et al., 1990).

However, also this line of reasoning is not conclusive because the *dependency* of the end-state comfort effect on precision requirements does not imply that precision requirements *cause* the end-state comfort effect. The following two points illustrate this argument. First, as an analogous case, consider the effect of object affordances on grasp selections (Herbort & Butz, 2011; c.f. Creem & Proffitt, 2001). For example, when participants grasp an upright mug to rotate it, the rotation task requires an initial uncomfortable grasp but the mug's affordance suggests an initial comfortable grasp (Herbort & Butz, 2011). In this case, the competing affordance reduces the end-state comfort effect. But although object affordances modulate the end-state comfort effect, it obviously cannot be argued that affordances drive the emergence of the end-state comfort effect. Likewise, although precision requirements modulate the end-state comfort, it cannot be concluded that they elicit it. Second, other variables may be confounded with precision requirement. For example, increasing the difficulty of the object manipulation's initial phase increases the duration of the initial phase. When participants then use comfortable initial grasps more frequently, they might well do this to reduce the time in awkward postures.

In summary, evidence in line with the precision hypothesis has been collected. However, it seems premature to conclude that precision is the "primary determinant" (p. 928, Rosenbaum et al., 2012) of grasp selections, as implied by the precision hypothesis, because both lines of evidence suffer from the problem that the level of control associated with specific postures could not be dissociated from other properties, such as comfort.

A third limitation is that the precision hypothesis hinges on the assumption that the control requirements of placing an object are typically higher than those of grasping and lifting it. However, accuracy requirements for the different movement phases have not been quantified in a meaningful way in typical object manipulation tasks. That is, whether grasping a specific object requires more control than placing and releasing it, and how both quantities should be compared in the first place, are yet open issues. Thus, despite its apparent validity, even this central assumption of the precision hypothesis remains yet to be tested in commonly used tasks.

Current Experiments

In this article, we directly test whether grasps are preferred for object manipulations that maximize the control over the hand and the object at that part of a movement where precision requirements are highest (precision hypothesis). To this end, we used a virtual reality (VR) setup, in which participants controlled a virtual hand to grasp and manipulate virtual objects. This approach allows to rule out the caveats of previous experiments. First, the controllability associated with an arm posture can be dissociated from its other properties, such as comfort. This allows us to directly test whether inducing differences in the controllability of different arm postures elicits grasp selections that maximize control. Second, as grasping and manipulating objects occurs in VR, the accuracy requirements of the various phases of the movements can be objectively defined.

In the VR environment, participants had to either move (translation) or rotate a bar by 180° (rotation) in a scenario, in which grasping always required less precision than placing the object. The bar could be grasped with either a more supine (clockwise rotated) or more prone (counterclockwise rotated) right-hand grip. The relationship between posture and control was manipulated by changing the gain between real and virtual hand movements (c.f. Potts et al., 2017) depending on the current arm posture. In one condition, the virtual hand could be better controlled in a prone posture than in a supine posture. If the precision hypothesis is correct, participants should favor a prone grasp for translations and a supine grasp for rotations because this maximizes control at the end of the object manipulation. In another condition, the most precise movements could be exerted in supine postures. Under such condition, we expect that participants use supine grasps for object translations and prone grasps for object rotations, which again maximizes control in the end-state.

As the precision hypothesis has not been directly tested in such a way, we initially created experimental conditions in favor of the precision hypothesis. First, the bar was presented in an orientation in which participants had no clear preference for a prone or supine grasp (neutral bar orientation). This should reduce the effect of habitual grasp selection strategies and largely equate the arm's natural controllability and comfort in the postures for grasping and placing. Second, placing the object was more difficult than grasping it. Hence, control was more important at the end of the object manipulations. Third, we emphasized movement accuracy in the instructions.

In the following, five experiments are reported. Exp. 1 is a manipulation check of the posture-dependent gain manipulation. Exps. 2 and 3 tested whether participants select grasps that maximize the control at the end of an object manipulation. Exp. 4 compared the artificial effect of the gain manipulation on control to the natural effect of adopting comfortable versus uncomfortable end-states. Exp. 5 tests whether participants use grasps that maximize control at the end of the object manipulation although this requires inverting the end-state comfort effect.

General Method

Participants

The number of male and female participants, their handedness (Coren, 1993), age, and the type of compensation are summarized in Table 1 for all experiments. All experiments have been approved by the ethics committee of the Department of Psychology of the Julius-Maximilians-Universität Würzburg (GZEK 2018-10; "Objektmanipulation in der virtuellen Realität").

We estimated the effect-size of the end-state comfort effect from an unpublished experiment, in which twelve participants either lifted a vertically oriented wooden bar or rotated it by 180° in altogether 64 trials. Participants ended comfortable in 75.2 % of trials (lifting: *M* = 98.7%, *SD* = 2.8%; rotation: *M* = 51,6%, *SD* = 37.6%), corresponding to other reports (Hughes et al., 2012; Seegelke, Hughes, & Schack, 2011). The size of the effect of the object movement on the percentage of prone grasps was $d_z = 1.3$. Assuming a comparable effect of the gain manipulation, the present experiments had a power of .88 to .98 to detect such an effect (α=.05).

Stimulus and Apparatus

Participants were standing, wore an HTC Vive (HTC Corporation, New Taipei City, Taiwan) head-mounted display (HMD), and wielded a wireless hand-held controller with the right hand. The HMD immersed the participants in a VR environment (Figure 1a, supplemental video 1), in which participants stood on a green square (50 cm x 50 cm; units refer to distances in VR). A piece of rippled cardboard was fixed on the corresponding position on the real floor to help participants keep the position. The real-world position of the hand-held controller was translated into VR coordinates to display a stylized right hand, consisting of two cuboids for the thumb and fingers. A red sphere (radius 7.5 cm) was used to indicate the start position for the hand. The start position was determined individually for each participant before the experiment by asking them to put their right hand next to their body in a relaxed way. The average position of the start sphere in Exp. 1 was 76 cm above the ground, 28 cm to the right, and 1 cm in front of the center of the green square.

The to-be-manipulated object ("bar") consisted of a brown cuboid handle (2.5 cm x 2.5 cm x 10.0 cm). A blue and a yellow cylindrical "whisker" protruded from the small faces of the cuboid (length 25 cm, radius 0.125 cm). In some trials, a white prone or supine hand was grasping the bar and cued participants to also use a prone or supine grasp, respectively (*supine-cued* and *prone-cued* trials). In other trials, no such hand was shown and participants could freely select either a supine or prone grasp (*neither-cued* trials).

The target consisted of a blue and a yellow disk (thickness 2.0 cm, radius 2.5 cm). The disks were positioned at a distance of 64 cm along a virtual axis. The position of the target disks was individually determined by asking participants to stretch out their right arm horizontally. On average, the target object was placed 62 cm before, 141 cm above, and 15 cm to the right of the center of the green square in Exp. 1.

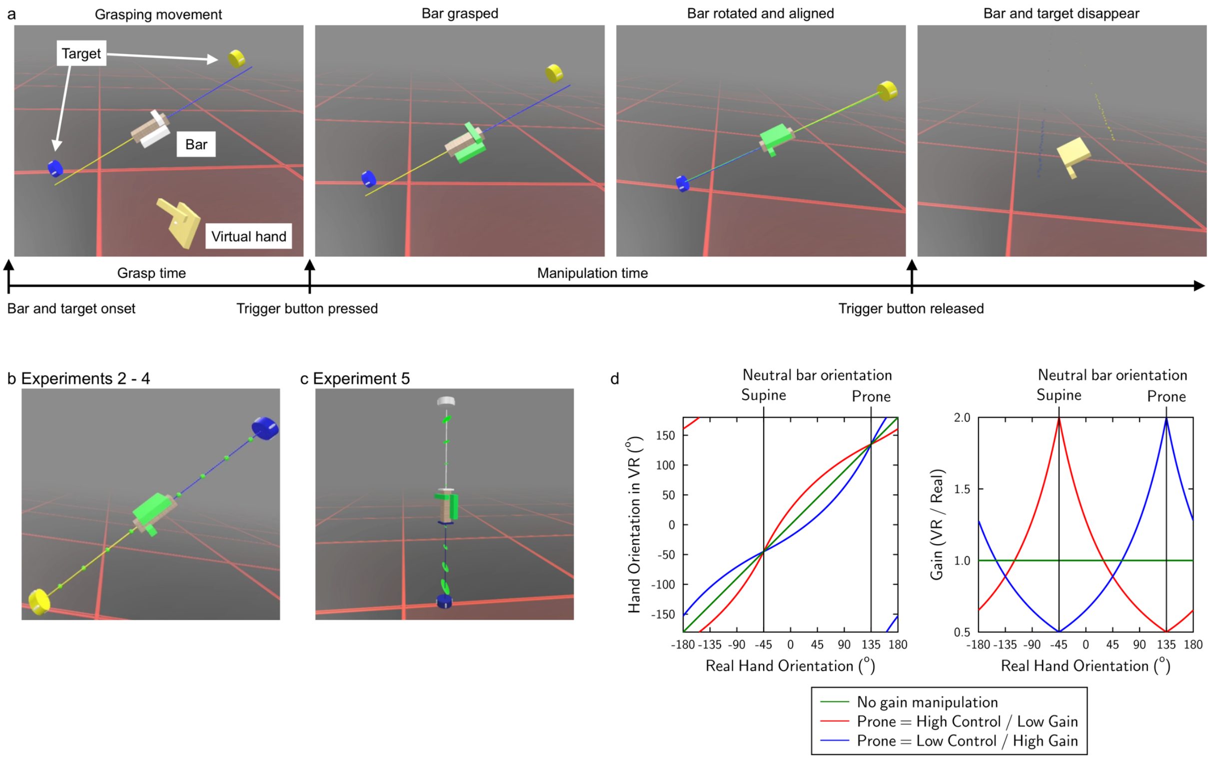

Figure 1. a) The sequence of events in a (supine-cued) trial. Annotations were not visible in the experiment. The white hand around the bar was rotated in 180° in prone-cued trials and not shown in neither-cued trials. In the depicted trial, the participant uses a supine initial grasp and adopts a prone end-state. b) Screenshot shortly before placing the bar in Exps. 2-4. c) Screenshot shortly before placing the bar in Exp. 5. d) The figure shows three possible mappings between real and virtual hand orientations (left) and the resulting gains (right). The green line indicates no gain-manipulation, in which the virtual hand orientation is identical to the real hand orientation. The other lines show the real-to-virtual hand orientation mapping when the prone neutral posture is associate with high (red) or low (blue) control, assuming the neutral bar orientation is 135°. In these cases, the gain and thus the controllability of the virtual hand depends on the real hand orientation.

Trial procedure

Figure 1a shows the trial procedure. Screen recordings of the trial sequence are provided as supplemental video 1. At the beginning of each trial participants had to stand over the green square (x and z coordinate of HMD within 30 cm of center of green square) and put the hand within the start sphere. When this was not the case for 4 seconds, a text instructed participants to assume a correct start position. A vibration of the controller indicated when the hand was in the start sphere.

When participants assumed the start position for 1.5 s, the bar and the target appeared and a beep sound was played. The bar was presented 10 cm in front of the target. Participants could grasp the bar by first moving the hand toward it and by then pressing and holding the controller's trigger button with the index finger of the right hand. The bar could only be grasped when the center of the hand was within an invisible cylinder surrounding the bar (r = 2.0 cm, l = 10 cm) and the orientation of the hand was within 10° of the bar orientation. To facilitate grasping, the virtual hand's color turned green when grasping was possible.

Once the bar was grasped it was aligned with and moved in synchrony with the virtual hand. Participants then positioned the bar between the target disks and released the trigger button. The bar was considered correctly placed, when the bar's center was within an invisible cylinder (r = 2.0 cm, l = 5.0 cm) in the middle between the target disks, when the bar orientation differed by no more than 2° from the orientation of the target axis, and when the colors of the whiskers matched the color of the target disks. To facilitate the cylinder placement, red translucent "laser beams" emanated from the center of the bar. The laser beams were parallel to the target axis and needed to be aligned with the whiskers. The beams were replaced by beads in Exps. 2-4 and disks in Exp. 5 (Figure 1b,c). When the bar was in the correct position and orientation, the laser beams turned green and the controller vibrated. When the trigger was released in this state, bar and target disks vanished in the distance with a swoosh sound (1 s). When the bar was not placed correctly at release, an error sound was played and the bar was reset to the initial position. Participants then had to re-grasp it and move it to the target again. This procedure was repeated until they managed to correctly place the bar. Participants were instructed to move swiftly but foremost accurately. Participants were informed that the movement of the virtual hand was distorted and that it could be controlled easier in some postures than in others. Moreover, participants were told that trials with errors had to be repeated later on.

Design

The trials presented during the experiments differed with respect to the prevailing posture-dependent gain manipulation, the orientation of the bar, the required object manipulation movement, and whether or not a specific grasp was cued.

Posture-dependent gain manipulations

During the experiment, the real-world hand orientation determined how easy or difficult it was to control the virtual hand. Control was manipulated by means of the gain between real and virtual hand orientations. The mapping from real-world hand orientations (pronation-supination range) to virtual hand orientations was distorted in such a way that large real-world hand rotations caused small virtual hand rotations (low gain / high control) for one specific real-world hand orientation and that small real-world hand rotations caused large virtual hand rotations (high gain / low control) for the exact opposite hand orientation. Intermediate hand orientations were associated with intermediate gains. Appendix A shows the equation for computing the distortion. No other aspects of the hand position or orientation were distorted.

The blue line in Figure 1d provides an example. When the real hand orientation is -45°, the gain between virtual and real hand orientations is only 0.5. That is, a 1° real word rotation causes a 0.5° virtual hand orientation. By contrast, when the real hand orientation is 135°, the gain is 2.0. Here, a 1° real-world hand rotation causes a 2° rotation of the virtual hand.

Individual mappings were generated for each participant. First, we determined a neutral bar orientation (see Part A: Determination of neutral bar orientation), for which the participant had no clear preference for the prone or supine grasps. Under one mapping, the gain was lowest in the (neutral) prone posture and highest in the (neutral) supine posture (*control-when-prone* = high). Under the other mapping, the gain was highest in the prone posture and lowest in the supine posture (control-when-prone = low). The mappings were always on during a block of trials (also, for example, when moving the hand to the start sphere).

Bar orientation, movement, and mode of grasp selection

The *orientation* of the bar and target could differ between trials (0° refers to a vertical bar orientation, negative signs denote clockwise rotations). The bar could be initially presented in alignment with the target, requiring a *translation* movement, or rotated by 180°, requiring a *rotation* (factor movement). Finally, the factor *grasp* was varied by prescribing a supine grasp (supine-cued) or prone grasp (prone-cued). Additionally, in other trials participants could freely choose between a prone or a supine grasp (neither-cued).

Experimental procedure

Part A: Determination of neutral bar orientation

The neutral bar orientation was determined in part A of the experiment, at the beginning of the first session. In this part, the hand orientation was not distorted (no gain manipulation). Participants received six blocks of translation trials, in which they could freely select a grasp. In each block, the bar orientations from -105° to -15° (Exp. 1) or 30° (Exps. 2-4) in 15° steps were presented in random order. The grasp selections from the second block on were used to compute the *neutral bar orientation* by fitting a logistic function to the function from bar orientations to the percentage of supine grasps using maximum likelihood estimates. The bar orientation at which the fitted logistic function revealed equal preference for a prone and supine grasp was considered the neutral bar orientation. The neutral bar orientations are listed in Table 1.

Part B and C: Exposure to posture-dependent gain manipulations

In part B, the virtual hand orientation was subjected to one of the posture-dependent gain manipulations. For one half of the participants, control in prone hand orientation was high, for the other half, it was low. Part C was identical to the part B, except that participants now received the posture-dependent gain manipulation that they were not yet exposed to. Bars were presented in the neutral orientation. Half of the scheduled trials were always rotation trials and half were translation trials. The number of supine-, prone-, and neither-cued trials per block are listed in Table 1 for each experiment. Trials with errors were repeated at a random position within the same block. Thus, the total number of administered trials exceeded the number of scheduled trials. Part B and C were divided in several blocks, which were separated by self-paced breaks in which participants received feedback about the number of errors. Which side of the target was blue and yellow and the order of the presentation of the two posture-dependent gain manipulations were counterbalanced over participants. The average durations of the sessions are shown in Table 1. Except for Exp. 1, part A and B were administered in the first session and part C on the second session on another day.

Data reduction and analysis

The following dependent variables were extracted from prone-cued and supine-cued trials (cf. Figure 1a). The *grasp time* was defined as the interval between the first time the hand's distance from its position at target onset exceeded 5 cm, and the time when participants successfully grasped the object. The *manipulation time* was the interval from grasping the object to releasing the object. The *total time* is the sum of the above variables. The percentage of *trials with errors* is the percentage of trials in which participants made at least one error. From the neither-cued trials, the percentage of *prone initial grasps* was extracted.

The trials for determining the individual bar orientations and warm-up trials were not further analyzed. The number of trials performed after warm-up, the percentage of trials in which participants made at least one error, and the percentage of temporal outliers in error-free trials (manipulation time differed by more than three standard deviations from the mean of the respective trial type) are provided in Table 1 for each experiment. Note that the task was deliberately made difficult to emphasize the accuracy requirements. All trials were considered for the computation of the percentage of errors, all error-free trials were considered for the analyses of grasp selections, and all error-free trials except outliers entered the analyses of grasp time, manipulation time, and total time.

Table 1
Summary of Experiments 1 - 5

	Experiment				
	1	2	3	4	5
Participants					
Number of females / males	7/5	5/3	7/5	10/2	9/3
Mean age (SD)	26 (4)	26 (7)	26 (4)	27 (9)	26 (8)
Right-handed / ambidextrous	12/0	8/0	12/0	12/0	11/1
Compensation (CC = course credit)	7€ or CC	15€ or CC	15€ or CC	14€	14 or CC
Design					
Number of sessions (days between sessions)	1	2 (3.6)	2 (6.0)	2 (6.2)	2 (2.7)
Blocks in part A / B / C	6/4/4	6/10/10	6/10/10	6/8/8	-/8/8
Scheduled trials (cued grasps) per block in part B and C[a]	supine: 10 prone: 10	neither: 20	supine: 4 prone: 4 neither: 16	-150°: 2 -120°: 2 ... 180°: 2	uncomfortable: 4 comfortable: 4 neither: 16
Duration, valid trials, neutral bar orientation					
Mean duration of session 1 / 2 (min)	42	39 / 31	49 / 43	43 / 34	26 / 24
Mean number of trials after warm-up (SD)	215 (30)	474 (20)	585 (40)	455 (37)	412 (16)
Percentage of trials with errors	25.6%	15.5%	18.0%	15.7%	6.8%
Percentage outliers	2%	-	2%	2%	1%
Mean neutral bar orientation (SD)	-49° (22°)	-64° (19°)	-50° (18°)	-63° (22°)	-

[a] 50% were translations and 50% were rotations.

Experiment 1

The aim of Exp. 1 was to assert that the posture-dependent gain manipulation that was used to manipulate the controllability of the hand actually determined which grips maximize control. We expected the shortest grasp times when the grasp can be executed with a high-control posture. We expect shorter manipulation times, shorter total times, and less errors when the end-state is associated with a high level of control.

Method

Two participants for whom no neutral bar orientation could not be determined were replaced. A warm-up block with the four different trial types preceded part B and C.

Results and Discussion

To facilitate the interpretation of the data, we recoded the factor grasp into the factor *control in end-state*. This factor indicates, whether the posture at the end of the object manipulation was associated with a high or low level of control. Significant results of repeated measures ANOVAs with the factors movement (translation vs. rotation), control-when-prone (high vs. low), and control in end-state (high vs. low) for each dependent variable are summarized in Table 2. Marginal effects are printed in grey and displayed in parenthesis. The expected effects are printed bold. Figure 2 shows the results.

All expected effects were found. Grasps times were shorter when participants grasped the bar with a high control posture (i.e. high control end-state for translations and low control end-state for rotations), as signified by the interaction between control in end-state and movement. Importantly, manipulation times, total times, and the percentage of trials with errors were smaller when the object manipulation ended in a high control posture. Figure 2b-d confirms that this was the case regardless of the movement or the actually used grasp. Additionally, grasps and manipulations were executed faster in translation trials.

In summary, bar manipulations were always faster and resulted in less errors, when the initial grip resulted in a high control end-state, irrespective of the type of grasp, the type of movement, or the type of the gain manipulation. The posture-dependent gain manipulation proved thus suitable to manipulate whether prone or supine postures maximize control.

Table 2

Significant effects of ANOVA with factors control in end-state (CE), Movement (M), and control-when-prone (CP) for Experiment 1

	Grasp time[a]			Manipulation time[b]			Total time[c]			Trials with errors[d]		
Effect	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p
CE		-		**29.0**	**< . 001**	**.73**	**21.0**	**.001**	**.66**	**18.9**	**.001**	**.63**
M	5.5	.039	.33	69.3	< .001	.86	95.6	< .001	.90		-	
CP		-			-			-		(3.8	.077	.26)
CE x M	**91.5**	**< .001**	**.89**		-			-		(3.74	.079	.25)
CE x CP	(3.3	.096	.23)		-			-			-	
M x CP		-			-			-			-	
CE x M x CP	-			-			-			-		

[a] All other *p*s $\geq .145$; η^2_ps $\leq .18$. [b] All other *p*s $\geq .133$; η^2_ps $\leq .19$. [c] All other *p*s $\geq .164$; η^2_ps $\leq .17$. [d] All other *p*s $\geq .144$; η^2_ps $\leq .18$.

Predicted effects are printed bold.

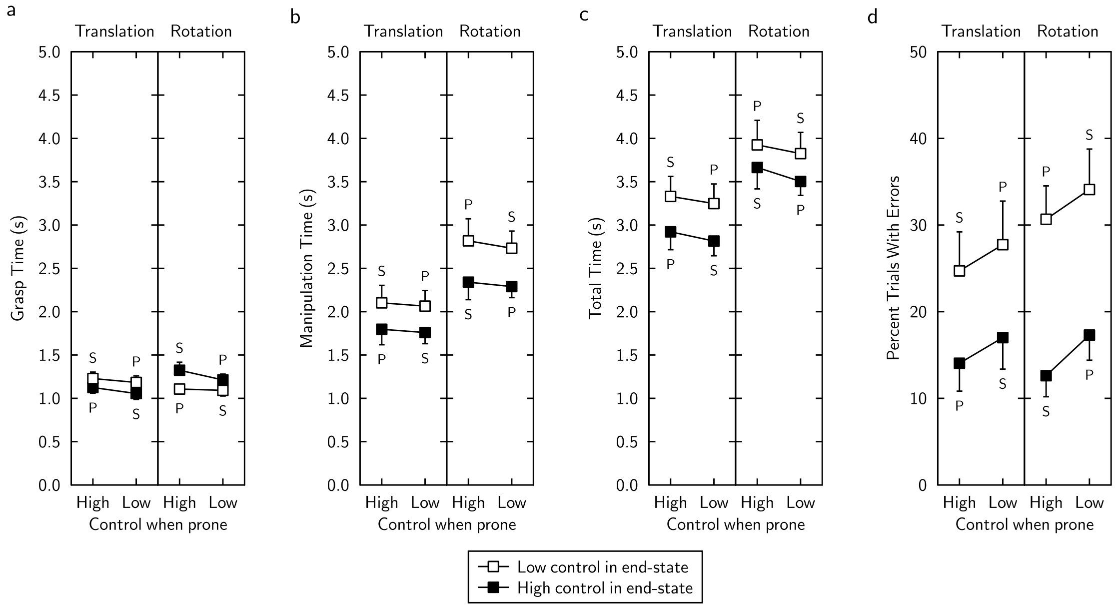

Figure 2. The chart shows movement times and errors of Exp. 1. The used grasps are indicated with the letters P (prone) and S (supine) next to each data point. Error bars show 1 s.e.m.

Experiment 2

Exp. 2 was conducted to test the precision hypothesis. We employed the setup of Exp. 1 but now allowed participants to freely choose how to grasp the bar. That is, only neither-cued trials were presented. If the precision hypothesis is correct, we expect that participants select grasps that result in high-control end-state. That is, when prone postures maximize control, participants should select prone grasps for translations and supine grasps for rotations. When supine postures maximize control, participants should select supine grasps for translations and prone grasps for rotations. Additionally, as we expect that extended exposure to the different gain-manipulations is necessary, this pattern of result should increase over time. That is, we expect an interaction between the factors movement, control-when-prone, and block. The predicted effect is charted in the insets of Figure 3.

Method

The laser beam indicating the correct bar orientation in Exp. 1 was replaced by a line of four beads on each side of the bar (radius 0.5 cm, positions 6.7, 13.3, 20.0, 26.7 cm from bar center, Figure 1b). The beads were always oriented in parallel to the target axis but moved in synchrony with the bar. The beads appeared whenever the bar was at the correct position and their color (red or green) indicated whether the bar was correctly oriented. The beads were introduced to facilitate the sagittal alignment of the bar and to provide a more intuitive alignment help. At the beginning of Part B and C, a block of four warm-up trials was administered.

Results and Discussion

The average percentages of prone initial grasps are shown in Figure 3. The data were entered in a repeated-measures ANOVA with factors control-when-prone (high vs. low), movement (translation vs. rotation), and block (mean of block 1 and 2 vs. mean of block 9 and 10). There were no significant main effects or two-way interactions, all *p*s $\geq .437$, all η^2_ps ≤ 0.09. The expected interaction between movement, control-when-prone, and block approached significance, $F(1,7) = 5.20$, $p = .057$, $\eta^2_p = .43$. That is, the frequency of high-control end-states tended to increase from the initial to the final two blocks. To explore whether grasp selections differed after exposure to the different gain manipulations, a repeated measures ANOVA with the factors of control-when-prone (high vs. low) and movement (translation vs. rotation) was conducted on the data of the last two blocks. The ANOVA revealed no significant main effects, both *p*s $\geq .320$, both η^2_ps ≤ 0.14. The interaction was not significant, $F(1,7) = 2.05$, $p = .195$, $\eta^2_p = .28$.

We further analyzed the data on an individual level (see supplement Figure ESM-1 for participant-wise plots). For each participant, we tested whether the frequency of supine and prone grasps in the last two blocks depended on whether a supine or prone grasp yielded higher control at the end-state. Fisher's exact test revealed that this was the case for two participants, both two-sided *p*s $\leq .001$ (all other *p*s = 1.000). Of the remaining six participants, five participants used different grasps for rotations and translations. The relationship between grasps and movements was perfectly consistent within participants (all *p*s $< .001$) but differed between them. The remaining participant always used a supine grasp.

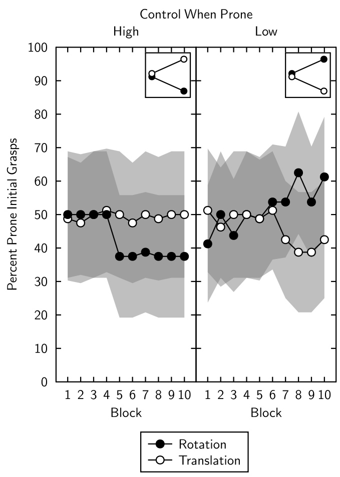

Figure 3. The chart shows the percentage of prone initial grasps over blocks in Exp. 2. The shaded area shows 1 s.e.m. The insets show the predicted effects.

Exp. 2 did not provide support for the precision hypothesis. This was the case although participants performed over 200 trials under each posture-dependent gain-manipulation and precision was emphasized by instructions and the consequences of errors. The analysis of individuals showed that the majority of participants (7 out of 8) adapted the grasp to different object manipulation tasks very consistently, implying that grasps were adjusted to the upcoming object manipulation. However, only two participants selected grasps that resulted in the end-state with a higher level of control. Of course, the sample size of the experiment was too small to refute any influence of the posture-dependent gain manipulations Nevertheless, precision requirements were clearly not a *primary determinant* of grasp selections as suggested by the precision hypothesis.

At this point the precision hypothesis cannot be rejected because several factors may have thwarted participants' adaptions of grasps to the different posture-dependent gain manipulations. First, as the correlation between postures and control is likely rather constant over extended periods of time or even over most of the life span, participants may have attributed difficulties in positioning the object to other factors (task constraints, unfamiliarity with VR, clumsiness). Moreover, many participants almost exclusively used a specific grasp for a specific movement, possibly because these grasps have been proven useful in years of day-to-day object interactions. For those participants, it might have been nearly impossible to discover that other grasps may have been more effective.

Experiment 3

In Exp. 3, we wanted to rule out the caveats of Exp. 2 and further facilitate adaptation to different posture-dependent gain manipulations. For this reason, we introduced four changes. First, we informed participants which postures increased or decreased control. Second, neither-cued trials were intermixed with prone-cued and supine-cued trials so that participants experienced the effects of different grasps on the object manipulation performance and could adapt grasps accordingly. As a side effect, this allowed us to check the effect of different grasp types once more. Third, we encouraged participants to try out how the virtual hand moves in different postures in the warm-up trials. Fourth, we added text messages at the end of each trial to further emphasize the importance of accurate object manipulations.

Method

Exp. 3 used the same general setup as Exp. 2 with the following exceptions. On trials without errors, the text "Well done!" (Translation of the German text "Gut gemacht!") was displayed when the bar was released. When participants finally released the correctly placed bar on trials with at least one error, participants were informed by a text message that there were errors before and that the trial was to be repeated later on. Before part B and C, participants were informed about the nature of the posture-dependent gain-manipulation. For example, when prone grips were associated with high control, they were told that they could control the hand orientation more accurately when the hand was rotated counterclockwise and that control over the hand rotation was reduced when the hand was rotated clockwise. Warm-up blocks with four neither-cued and four prone- or supine-cued trials were administered before part B and C.

Results and Discussion

Figure 4a shows the average percentage of prone initial grasps in the neither-cued trials. This variable was entered in a repeated-measures ANOVA with factors of control-when-prone (high vs. low), of movement (translation vs. rotation), and of block (1+2 vs. 9+10). Descriptively, prone initial grasps were more frequently for translations than for rotations, $F(1,11) = 3.51$, $p = .088$, $\eta^2_p = .24$. Control-when-prone and movement interacted, $F(1,11) = 15.38$, $p = .002$, $\eta^2_p = .58$. The interaction between block and control-when-prone approached significance, $F(1,11) = 4.471$, $p = .058$, $\eta^2_p = .29$. Importantly, the three-way interaction was significant, indicating that the percentage of object manipulation that ended in a high-control posture increased over blocks, $F(1,11) = 7.18$, $p = .021$, $\eta^2_p = .40$. There were no other significant effects, all ps $\geq .712$, all η^2_ps ≤ 0.01. To follow up on this result, a repeated measures ANOVA with factors control-when-prone and movement was conducted on the data of the last two blocks of each session. No significant effects of control-when-prone, $F(1,11) = 1.41$, $p = .260$, $\eta^2_p = .11$, or movement were found, $F(1,11) = 2.94$, $p = .115$, $\eta^2_p = .21$. Importantly, both factors interacted, $F(1,11) = 21.09$, $p = .001$, $\eta^2_p = .66$. This confirms that grasps were selected that allow for a high level of control at the end of the object manipulation, irrespective of whether the manipulation was a translation or rotation or whether the required grasp was prone or supine. Additionally, we analyzed participants sensitivity toward the gain manipulation on an individual level (data of individual participants are provided in ESM-1). For each participant, we tested whether the frequency of different grasps in the last two blocks depended on which grasp yielded a high-control end-state. Fisher’s exact test revealed that this was the case for nine of the twelve participants, all two-sided ps $\leq .039$. Of the remaining three participants, only one participant consistently selected different grasps for different movements, according to Fisher’s exact test, $p < .001$ ($p \geq .492$ for the other two participants).

As a manipulation check, we analyzed grasp time, manipulation time, total time, and the percentages of trials with errors in the trials in which a specific grasp was cued (Figure 4b-e). As in Exp. 1, we recoded the factor grasp into the variable control in end-state. Table 3 shows significant effects revealed by repeated measures ANOVAs with the factors of movement (translation vs. rotation), control-when-prone (high vs. low), and control in end-state (high vs. low). Expected effects a printed bold. The data are shown in Figure 4b-e.

All expected effects were found. Grasp times were shorter when the bar was grasped with a high-control posture, as indicated by the interaction between control in end-state and movement. Manipulation times, total times, and the percentage of trials with errors were smaller when the object manipulation ended in a high-control posture. This was the case, regardless of the type of grasp, the type movement, or the type of the gain manipulation, confirming the effectivity of the gain manipulation. Additionally, grasp times, manipulation time, and total time were greater for rotations than for translations. These variables were further modulated by a three-way interaction, which seemed to emerge because of a general advantage of prone grasps.

Table 3

Significant effects of ANOVA with factors control in end-state (CE), Movement (M), and control-when-prone (CP) for Experiment 3

	Grasp time[a]			Manipulation time[b]			Total time[c]			Trials with errors[d]		
Effect	*F*(1,11)	p	η^2_p	*F*(1,11)	p	η^2_p	*F*(1,11)	p	η^2_p	*F*(1,11)	p	η^2_p
CE		-		**54.2**	**< .001**	**.83**	**44.8**	**< .001**	**.80**	**51.0**	**< .001**	**.82**
M	7.4	.020	.40	330.8	< .001	.97	327.1	< .001	.97	(4.3	.061	.28)
CP		-			-			-			-	
CE x M	**24.1**	**< .001**	**.69**		-			-			-	
CE x CP		-			-			-			-	
M x CP		-			-			-			-	
CE x M x CP	5.2	.044	.32	6.1	.032	.36	8.0	.016	.42		-	

[a] All other *ps* ≥ .416; η^2_ps ≤ .06. [b] All other *ps* ≥ .145; η^2_ps ≤ .18. [c] All other *ps* ≥ .284; η^2_ps ≤ .10. [d] All other *ps* ≥ .228; η^2_ps ≤ 0.13.
Predicted effects are printed bold.

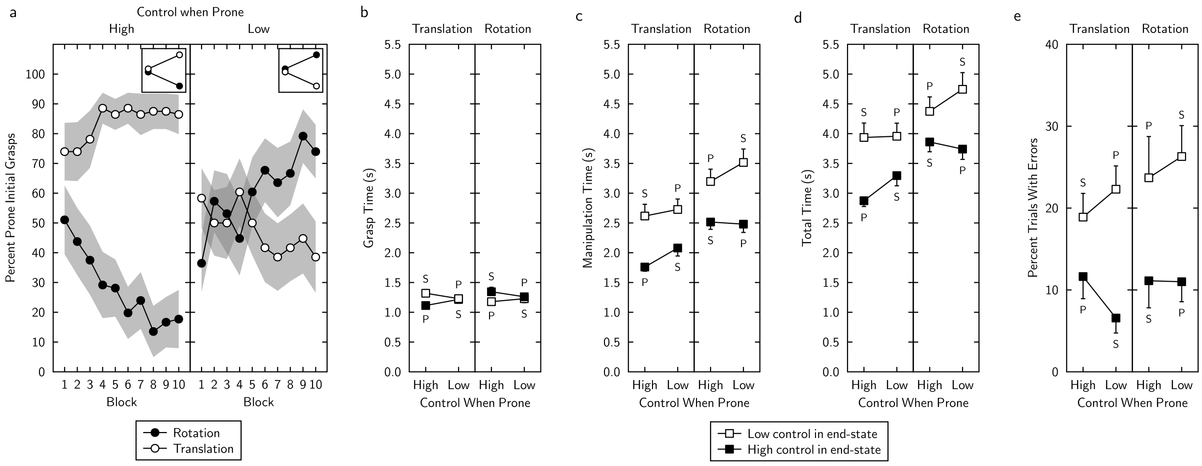

Figure 4. The charts show the percentage of prone initial grasps (a), movement time (b-d) and errors (e) in Exp. 3. The insets in a) depict the predicted interaction. The letters in b)-e) indicate whether a data point reflects prone (P) or supine (S) initial grasps. The shaded area (a) and error bars (b-e) shows 1 s.e.m.

The results of Exp. 3 support the precision hypothesis. Most participants positioned the object while being in a high-control end-state. However, in conjunction with Exp. 2, it also became apparent that controllability only affected grasp selections under very specific conditions. Participants needed to be informed about the effect of the posture on the controllability of the hand or had to use different grasps throughout the experiment. Even then, grasps were only adapted relatively slowly to the gain manipulations over the course of many trials.

Experiment 4

In Exp. 3, we induced differences in the controllability of specific prone and supine postures and, as a result, some grasps allowed for more efficient object manipulations than others. In Exp. 3, the magnitude of the benefits of selecting the more suitable grasp $B_{induced}$ (e.g., expressed in errors) sufficed to elicit grasp selections that were analogous to the end-state comfort effect (i.e. different grasps were used for translation and rotation). As it can be assumed that grasp selections would have remained unaffected when the gain manipulation would have been much subtler and $B_{induced}$ thus much smaller, we now address the question how strongly control is improved by adopting comfortable end-states due to the natural, biomechanical differences in control associated with comfortable and uncomfortable postures. If the benefits of showing the end-state comfort effect ($B_{natural}$) were much smaller than $B_{induced}$, it could be doubted that the enhancement of control resulting from the end-state comfort effect is large enough to elicit it. However, if $B_{natural}$ turns out to be about as great as $B_{induced}$, it appears much more plausible that the biomechanical controllability differences between comfortable and uncomfortable postures can elicit the end-state comfort effect outside the lab. Hence, Exp. 4 was conducted to compare the induced effect of our gain manipulation on controllability ($B_{induced}$) with the natural effect of adopting comfortable vs. uncomfortable end-states ($B_{natural}$).

Participants were asked to translate or rotate a virtual bar using specific, cued grasps while the gain was not manipulated. For analysis, we computed the performance benefits of showing the end-state comfort effect. These values were compared to the performance benefits of adopting high-control end-states in Exps. 1 and 3. If the benefits of adopting comfortable end-states are comparable in order of magnitude to the benefits of adopting high-control end-states, which have been shown to affect grasp selections in Exp. 3, we consider the precision hypothesis plausible. As the analysis focuses on the magnitude of the effects, we focus on a descriptive analysis.

Method

Exp. 4 reused the setup of Exp. 3 with the following modifications. No gain manipulations were administered in part B and C (that is, part B and C were identical). Two factors were varied. Grasps orientations of -150°, -120°, …, and 180° were cued. For each of the grasp orientations, the bar was oriented accordingly, and the blue or yellow end of the bar was close to the thumb with equal frequency. Additionally, rotations and translations had to be executed with equal frequency. Each trial type was scheduled once in block 1 and 2, 3 and 4, and so on. Four randomly selected warm-up trials were presented before part B and C. Trials on which the grasp time and the manipulation time exceeded more than three standard deviations from the respective mean were excluded.

To analyze the benefit of adopting a comfortable end-state, we defined the more medial grasps between the two neutral grasp orientations (-63° , 117°) as comfortable (-60°, -30°, … , 90°) and the remaining grasps as uncomfortable (-150°, -120°, -90°, 120°, 150°, 180°). This definition is relatively arbitrary for the -60° grasp, which is close to the average neutral grasp (-63°), but corresponds to subjective comfort ratings for the remaining grasps (Johnson, 2000; Rosenbaum et al., 1992). For each dependent variable, we subtracted the means from all trials with specific uncomfortable end-states from the means of the trials with the exact opposite, comfortable end-states (-120° vs. -60° , 150° vs. -30°, …). These differences express the benefit of showing the end-state comfort effect for different bar orientations. As a comparison, we computed the differences between grasps with a low-control and high-control end-state for each of the dependent variables in Exps. 1 and 3. As the aim of the analysis is to compare the order of magnitude of these effects we rely on a descriptive analysis.

Results and Discussion

Figure 5 shows the benefits of comfortable end-states in Exp. 5 and the benefits of high-control end-states in Exps. 1 and 3. Not surprisingly object translations were executed faster in comfortable postures. The benefits depended on the differences in comfort between the involved grasps. More interesting are the object rotations. Not surprisingly, showing the end-state comfort effect slows down grasp times. Manipulation times and the percentage of errors were reduced by adopting a comfortable end-state. Here, for a bar orientation of 30°, the benefits of showing the end-state comfort effect are at least as large as adopting a high-control end-state in Exps. 1 and 3. The reduction of errors associated with showing the end-state comfort effect in the more common scenario of the rotation of a vertically oriented object (0°) were typically smaller but still comparable to the benefits of adopting high-control end-states. An unexpected finding was that the type of the grasp affected the grasp time about as much as the manipulation time. Consequently, the benefit of comfortable end-states for the total time were inconsistent and relatively small compared to the effects of the gain-manipulation in Exps. 1 and 3.

In summary, Exp. 4 confirmed that the benefits of adopting comfortable end-states was comparable to the effect of adopting high-control end-states in Exps. 1 and 3. As these effects were sufficient to change grasp selections in Exp. 3, it seems fair to argue that the comparable benefit of a comfortable end-state likewise suffices to elicit the end-state comfort effect.

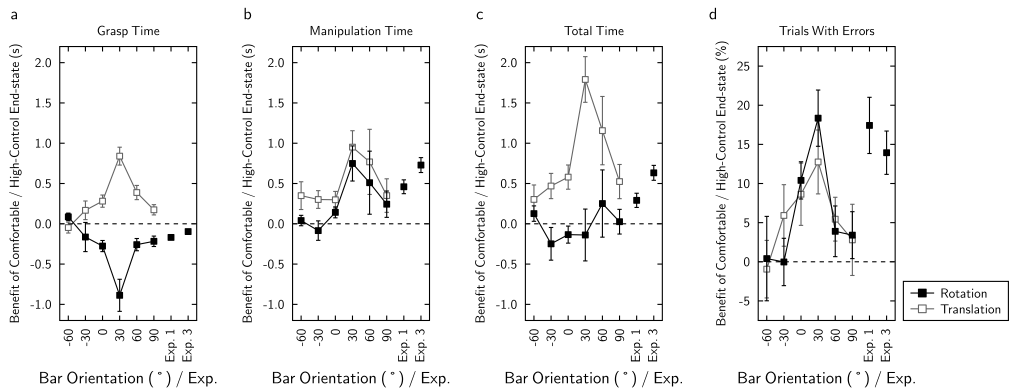

Figure 5. a-d) The charts show the benefits of adopting a comfortable end-state for various bar orientations and of adopting a high-control end-state in Exps. 1 and 3. Error bars show 1 s.e.m.

Experiment 5

In Exp. 3, the bar was intentionally presented in a neutral orientation, in which participants preferred neither grasp a priori and prone end-states were about as comfortable as supine end-states (Johnson, 2000; Rosenbaum et al., 1992). Exp. 3 thus showed that controllability affects grasp selections when comfort is held constant, leaving open the question whether comfort or correlated variables could be more potent determinants of grasp selection than control. In Exp. 5, we now tested whether participants also select grasps that maximize control at the end of the object manipulation when this requires adopting uncomfortable end-states. In Exp. 5, we asked participants to translate or rotate vertically oriented bars (0°) under two gain manipulations. We expect that participants show a typical end-state comfort effect in the initial block. Under one manipulation, control over the hand was enhanced in comfortable postures and reduced in uncomfortable postures. We expect that participants clearly prefer grasps that allow them to place the object with a comfortable and high-control arm posture in this condition at the end of the session. That is, we expect an increase of the end-state comfort effect. More critically, under the other manipulation, the hand could be best controlled with uncomfortable postures. If the precision hypothesis is valid, we expect that participants select grasps that allow ending the object manipulations in an uncomfortable posture in this condition – thus ideally inverting the end-state comfort effect. The predicted effects are shown in the insets of Figure 6a.

Method

Exp. 5 was based on Exp. 3 with the following changes. The yellow color of the bar and target was now replaced by white and the handle was lined with small blue or white plates to make the bar and target orientation more salient (Fig. 1c). Once the participants were in the start position for 250 ms the bar and the target appeared but were out of reach. When the participants stayed in the start position for another 1000 ms, bar and target jumped 50 cm toward the participant to a position that was individually determined at the beginning of the first session as in the other experiments. Otherwise, bar and target disappeared until participants assumed the start position for 250 ms again. This change was introduced to give participants time to identify the required object manipulation (and grasp). The beads were replaced by elliptical disks (Fig. 1c). The axes of the ellipses span an angle of 4° from the center of the handle in the left-right dimension and 20° in the front-back dimension. The target was considered hit when the overall angle between bar and target was below 10° and below 2° in the pronation-supination dimension. Thus, a high degree of precision was only required in the dimension that was subjected to the gain-manipulation.

Part A was not administered. Participants were exposed to two different gain-manipulations in part B and part C. The highest and lowest gains were now always associated with hand orientations of 0° and 180°. In the following, we refer to the 0°-grasp as comfortable and the 180°-grasp as uncomfortable. In one control condition, the gain was highest when the hand orientation was 0° and lowest when it was 180° (control-when-uncomfortable = high). In the other control condition this pattern was reversed (control-when-uncomfortable = low). At the beginning of each session, four neither-cued trials, four random comfortable-cued or uncomfortable-cued trials, and sixteen translation trials (8 comfortable-cued, 8 uncomfortable-cued) were administered. The initial orientation of the target and the bar was counterbalanced over trial types within blocks.

Results and Discussion

Figure 6a shows the average percentage of comfortable initial grasps in the neither-cued trials over the blocks of each session. The percentage of comfortable initial grasps was entered in a repeated-measures ANOVA with factors of control-when-uncomfortable (high vs. low), of movement (translation vs. rotation), and of block (1+2 vs. 7+8). The percentage of comfortable initial grasps was higher when the uncomfortable grasp was associated with high control, $F(1,11) = 7.28$, $p = .021$, $\eta^2_p = .40$. A comfortable initial grasp was more frequent for translations than for rotations, $F(1,11) = 22.16$, $p = .001$, $\eta^2_p = .67$. Comfortable initial grasps were more frequent in the initial than in the final blocks, $F(1,11) = 12.89$, $p = .004$, $\eta^2_p = .54$. Control-when-uncomfortable and movement interacted, $F(1,11) = 11.10$, $p = .007$, $\eta^2_p = .50$. Importantly, the three-way interaction confirmed that participants increasingly adopted high-control end-states over the course of each session, $F(1,11) = 7.73$, $p = .018$, $\eta^2_p = .41$. There were no other significant effects, all ps ≥ .639, all η^2_ps ≤ .02. A follow-up repeated measures ANOVA with factors control-when-uncomfortable and movement was conducted on the data of the last two blocks of each session. No significant effect of control-when-uncomfortable emerged, $F(1,11) = 3.75$, $p = .079$, $\eta^2_p = .25$. Comfortable initial grasps were more frequent for translations than for rotations, $F(1,11) = 13.74$, $p = .003$, $\eta^2_p = .56$. As expected, both factors interacted, $F(1,11) = 13.49$, $p = .004$, $\eta^2_p = .55$. Thus, how grasps were adapted to upcoming object manipulations depended on the level of control associated with comfortable and uncomfortable postures.

As in Exp. 3, considerable inter-individual differences were observed (see supplement Figure ESM-1 for participant-wise plots). Seven participants selected predominantly comfortable grasp when a comfortable grasp resulted in a high-control end-state and uncomfortable grasps otherwise, Fisher's exact, all ps ≤ .007 (p = 1.000 for the other five participants). The remaining five participants consistently selected different grasps for translation and rotations irrespective of the gain manipulation, according to Fisher's exact test, all ps < .001.

We analyzed movement times and the percentages of trials with errors of the uncomfortable- and comfortable-cued trials (Figure 6b-e) to check whether the gain manipulation affected the optimal grasps. As in Exps. 1 and 3, we recoded the factor grasp into the factor control in end-state. Repeated measures ANOVAs with the factors of movement (translation vs. rotation), control-when-uncomfortable (high vs. low), and control in end-state (high vs. low) were conducted on each dependent variable. Significant effects are summarized in Table 4, expected effects are printed bold. Figure 6 shows the data.

Table 4

Significant effects of ANOVA with factors control in end-state (CE), Movement (M), and control-when-uncomfortable (CU) for Experiment 5

	Grasp time[a]			Manipulation time[b]			Total time[c]			Trials with errors[d]		
Effect	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p	$F(1,11)$	p	η^2_p
CE		-		**24.5**	**< .001**	**.69**	**24.5**	**<.001**	**.69**	**96.1**	**< .001**	**.90**
M	17.7	.001	.62	139.2	< .001	.93	176.8	<. 001	.94	(4.3	.062	.28)
CU		-			-			-			-	
CE x M	**15.4**	**.002**	**.58**		-			-			-	
CE x CU	(3.6	.083	.25)	(4.6	.056	.29)	(4.8	.050	.31)	5.1	.045	.32
M x CU		-			-			-			-	
CE x M x CU	48.8	< .001	.82		-		5.9	.033	.35		-	

[a] All other *p*s $\geq .253$; η^2_ps $\leq .12$. [b] All other *p*s $\geq .154$; η^2_ps $\leq .18$. [c] All other *p*s $\geq .389$; η^2_ps $\leq .07$. [d] All other *p*s $\geq .103$; η^2_ps $\leq .22$

Predicted effects are printed bold.

The analyses asserted that the gain manipulation was effective. The grasp time was on average shorter, when participants grasped the bar with a high-control posture, as revealed by the interaction between control in end-state and movement. The effect was further modulated by a three-way interaction due to an overall advantage of comfortable grasps. The manipulation time, total time, and percentage of trials with errors were always lower when the end-state was associated with high control. The interaction found for the grasp time was also reflected in total times. Moreover, the benefit of a high-control end-state was generally larger for rotations than for translation. Despite these modulating effects, Figure 6 shows that manipulation times, total times, and the percentage of errors were always lower when participants adopted a high-control end-state, irrespective of the specific posture, gain manipulation, or object manipulation task. Finally, grasps and manipulations were executed quicker in translation trials and at least numerically less errors were made in translation trials.

In conclusion, most participants selected grasps that maximized control at the end of the object manipulation. When the natural difference between comfortable and uncomfortable postures were amplified by the gain-manipulation, participants adopted comfortable end-state in 99% of trials. This percentage is considerably higher than the 60-70% that are usually reported in experiments that require rotations and translations of a vertical bar (e.g., Hughes et al., 2012; Seegelke, et al., 2011). When the control was enhanced in uncomfortable postures and reduced in comfortable postures, many participants preferred an initially comfortable grasp for object rotations. Five out of twelve participants even used an uncomfortable grasp for object translations. Thus, for the majority of participants, control was a more potent determinant of grasp selection than comfort or other properties associated with arm postures.

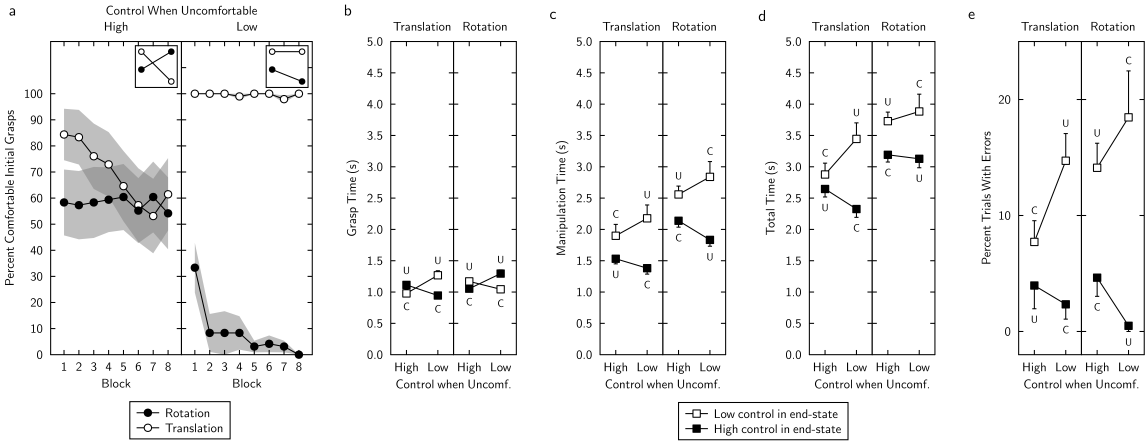

Figure 6. The chart shows the percentage of comfortable initial grasps (a), movement time (b-d) and errors (e) in Exp. 5. The insets in a) show the predicted effects. The initial grasps are indicated with the letters C (comfortable) and U (uncomfortable) next to each data point in b)-e). The shaded area (a) and error bars (b-e) shows 1 s.e.m.

Correlation Between Grasp Selections and the Benefits of Specific Grasps

Grasp selections may have differed between individuals because the gain manipulation may not have affected all participants alike. To examine this possibility post-hoc, we correlated the percentage of neither-cued trials with a high-control end-state (final two blocks of each session) with the decrease in total time and errors resulting from high-control end-states (difference between all trials with low-control vs. high-control end-state) in Exps. 3 and 5. Figure 7a shows that the more high-control end-states reduce the total time, the more frequently participants adopt high-control end-states. The Pearson correlation of the pooled data was $r = .70$, $t(22)=4.55$, $p < .001$. The individual correlations for Exp. 3 and 5 were also significant, Exp. 3: $r = .66$, $t(10) = 2.79$, $p = .019$; Exp. 5: $r = .72$, $t(10) = 3.32$, $p = .008$. Figure 7b shows that the benefit of high control end-states with respect to the percentage of trials with errors was uncorrelated with the percentage of high-control end-states, pooled: $r = .02$, $t(22) = 0.11$, $p = .915$; Exp. 3: $r = .16$, $t(10) = 0.50$, $p = .631$; Exp. 5: $r = -.22$, $t(10) = -0.70$, $p = .500$. However, as almost all participants benefitted from high-control end-states, this negative result may be a ceiling effect. In summary, the effectivity of the gain manipulation in Exps. 3 and 5 differed between participants. The more adopting a high-control end-state decreased movement times, the more likely it was that participants adopted high-control end-states. This accords with the precision hypothesis. Moreover, this also indicates that participants did not adopt high-control end-states because they assumed that this was expected by the experimenters, for example as a result of the instructions. Additionally, close visual inspection of Figure 7A reveals that participants only ended in high-control postures when the benefits in total times of these posture exceeded some positive value in both experiments. This small, descriptive bias against high-control end-states also suggests that grasp selections were not the result of any experimenter effects.

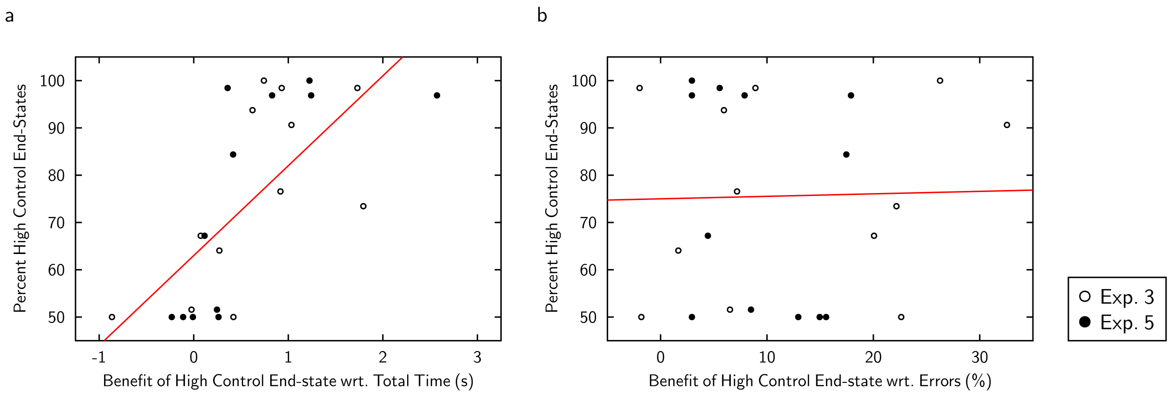

Figure 7. a,b) The chart plots the percentage of neither-cued trials with a high-control end-state against the benefits of high-control end-states in terms of total time / errors for the individual participants of Exps. 3 and 5. The red line shows a linear regression over the pooled data.

Discussion

According to the precision hypothesis, the end-state comfort effect emerges because objects can be controlled better with comfortable postures than with uncomfortable postures and control is typically most important at the end of the object manipulation. We experimentally manipulated the relationship between posture and control to test this hypothesis. Exp. 1 confirmed that our manipulation affected grasp times, manipulation times, total times, and percentage of errors as expected. Exp. 2 revealed no consistent effects of the controllability of the hand on grasp selections. Exp. 3 ruled out several aspects that may have thwarted the adaptation of the grasps to different gain manipulations in Exp. 2. In this experiment, participants increasingly selected grasps that maximized control at the end of the object manipulation. Exp. 4 showed that the natural benefit of adopting comfortable instead of uncomfortable end-states was comparable to the induced benefit of adopting high-control instead of low-control end-states. As the induced benefits sufficed to change grasp selections, the benefits between uncomfortable and comfortable postures can thus also be expected to determine grasp selections in day-to-day experience with object manipulations. Finally, Exp. 5 showed that the level of control associated with specific postures determined grasp selections even if this implied adopting uncomfortable postures at the end of object manipulations. Thus precision, rather than comfort or correlated variables, primarily determined grasp selections. In summary, the experiments provided direct support for the precision hypothesis.

Modification of the End-state Comfort Effect and Implications for Its Acquisition

The experiments have shown that it is comparably difficult to adapt one's grasp selections to changes in the relationship between arm-posture and the controllability of the hand. In Exps. 2, 3, and 5 participants repeatedly manipulated an object in just two different ways under highly controlled circumstances. Nevertheless, participants often only adapted their grasps to the gain manipulation after several blocks of trials. Moreover, such adaptations were frequently observed in Exp. 3 (75% of participants) and 5 (58%) but not in Exp. 2 (25%). The key differences between Exp. 2 and Exps. 3 and 5 were twofold. First, participants were made aware of the effects of posture on the controllability of the virtual hand in Exps. 3 and 5 but not Exp. 2. Second, participants necessarily experienced the effects of different grasps in Exps. 3 and 5 but not in Exp. 2. The inspection of the individual data suggests that some participants may have benefitted from the instructions and others from the requirement to use different grasps. Some participants adjusted their grasps to the gain manipulations from the first block on. This immediate effect can be attributed most likely to the information conveyed by the instructions. Other participants adapted their grasps to the gain manipulation only after several blocks. We suspect that the experience of the effects of different grasps drove adaptation in these participants. However, it is possible that they also additionally benefitted from the instructions, for example by drawing attention to the potential effects of assuming different postures.

These findings have implications regarding the acquisition of the end-state comfort effect. First, learning to select grasps that maximize control seems to be surprisingly difficult. Changing the relationship between hand controllability and arm posture alone was insufficient to induce changes in grasp selection for object manipulation, at least within a few hundred trials in Exp. 2. This mirrors other experiments showing that grasp selections are not easily adjusted to uncommon (e.g., sequential) object manipulations (Mathew, Kunde, & Herbort, 2017). The difficulties observed in the lab might be amplified in the natural environment because object manipulations are usually not repeated as frequently as in our experiments, which hinders the direct comparison of the effects of different grasps, and because the requirements of object manipulations typically differ considerably and might be best performed with different grasp selection strategies.

These considerations have implication for the development of the end-state comfort effect, which is only consistently shown from the age of ten years on (for a review see Wunsch, Henning, Aschersleben, & Weigelt, 2013). It has been speculated that the development of the end-state comfort effect is relatively protracted because younger children do not yet benefit from comfortable end-states (Rosenbaum, Herbort, van der Wel & Weiss, 2014; Zander, Weiss & Judge, 2013). The present data raise the possibility that the difficulty to learn how to plan for comfortable, high-control end-states may additionally prolong the acquisition of the end-state comfort effect. As already relatively young children frequently correct grasps that would result in uncomfortable postures (Adalbjornsson, Fischman & Rudisill, 2008; McCarty, Clifton & Collard, 1999) – suggesting that they prefer comfortable postures – this factor may even play a substantial role.

Second, the relationship between the arm posture and the controllability of the hand may define optimal grasps, but other factors are necessary for adapting ones grasp accordingly. To our knowledge, such factors have not been investigated directly but were nevertheless suggested in the literature. Rosenbaum and Jorgensen (1992) argued that grasps for object manipulations are repeated until feedback from an object manipulation signals the necessity to change the grasp (cf. Künzell et al. 2013, for a similar suggestion). This reasoning is in line with the experiment of Mathew and colleagues (2017), in which participants were asked to rotate an object first by a small angle (30°) in one direction and then

– without readjusting the grasp – by a larger angle (up to 180°) in the opposite direction. It was found that only a subset of participants adjusted their grasps to the second, larger object manipulation step. These participants were also more likely to have experienced relatively uncomfortable postures than their peers, possibly triggering a change in the grasp selection strategy. To conclude, future research on the modification or acquisition of the end-state comfort effect should not only focus on normative models of grasp selection. In addition, the cognitive factors that allow exploiting the benefits of specific grasps need to be considered.

Individual Differences

The end-state comfort effect notoriously differs between individuals (Hughes et al., 2012; Mathew et al., 2017; Rosenbaum et al., 1996; Seegelke, Hughes, Schütz & Schack, 2012). Whereas some participants consistently use different grasps for different tasks, others consistently do not. In Exps. 3 and 5, we did not only record grasp selections but also the effects of the grasps on performance. The data suggest that participants typically select grasps that optimize control (e.g. minimize total time) but that the optimal grasps differed between participants. Exp. 4 directly assessed the benefits of showing the end-state comfort effect. Although uncomfortable grasps decreased the *average* manipulation times and errors in rotation trials, not all participants benefitted from uncomfortable initial grasps. In the typical case of a 180° rotation of a vertical object, 25% of participants did not benefit from an uncomfortable initial grasp in terms of manipulation time. Likewise, the error rate was unaffected by another 25% of participants. Uncomfortable initial grasps even increased the total time for 58% percent of participants. This interindividual variability of the control benefits resulting from showing the end-state comfort effect may account for interindividual differences in grasp selections because optimizing control over the handled object may require different grasp selection strategies for different individuals. Thus, the absence of an effect of the object manipulation task on grasp selection of an individual participant may have little bearing on cognitive aspects of control, such as planning ability or sensibility to task changing demands (Hughes et al., 2012).

Effect of Precision Requirements

The precision hypothesis has previously been investigated by manipulating the precision requirements at the onset of the object manipulation relative to those at the offset while keeping the relationship between arm posture and control constant (Hughes et al., 2012; Künzell et al., 2013; Rosenbaum et al., 1990; Stöckel & Hughes, 2015). We used the complementary approach of keeping the precision requirements at the onset and offset of object manipulations constant but manipulated the relationship between arm postures and control. At the first glance, adaptation of the grasps appeared to be much slower in our experiments than in the former experiments. For example, in the study of Künzell et al., (2013), adaptation to new tasks asymptoted within three trials. In the other studies, effects of the precision manipulation were found although much fewer trials were administered. By contrast, adaptation to the gain-manipulation progressed over hundreds of trials in our experiment. However, this discrepancy is only apparent: Although adaptation progressed over many trials, grasps were affected by the gain manipulation from the first block on, at least in Exp. 5, with only eight rotation and eight translation trials. When the gain-manipulation favored a comfortable end-state, object manipulations ended with a comfortable posture in 83% of trials (SD = 17%). When the gain manipulation worked against the end-state comfort effect, the percentage of trials with a comfortable end-state was only 63% (SD = 33%). These values are surprisingly close to those from studies in which initial or final precision requirements were varied (Hughes et al., 2012; c.f., Stöckel & Hughes, 2015). Thus, grasp adaptations operated on the same time scale in the current and previous experiments. However, as our participants performed several blocks of trials and as some participants adapted to the gain manipulation only after a few blocks, the adaptation to the gain-manipulation continued over a longer period. It might be speculated that similar effects might have been observed in the earlier studies if more trials had been administered.

Limitations

The present experiments provided direct support for the precision hypothesis in a task that required the 180°-rotation of an objects. The experiments not only showed that precision is an important determinant of grasp selection in this task but that this factor is more important than other attributes that are correlated with the arm posture – such as comfort. However, it remains an open question whether other factors come into play in other types of object manipulations. One critical aspect may be whether the task requires a specific rotation direction or not. The end-state comfort effect is found less consistently in the employed 180°- rotation task (typically in 60%-70% of trials), which can be realized with clockwise and counterclockwise rotations, than in tasks that require or imply a specific rotation direction (Hughes et al., 2012). For example, when the task implies a clockwise or counterclockwise rotation of a bar or a knob, almost all (adult) participants consistently use different grasps for different rotation directions (e.g., Rosenbaum et al., 1990; Herbort, Büschelberger, & Janczyk, 2018). This suggests that additional constraints may be involved in such tasks. Whether these constraints are more potent than movement precision remains yet to be investigated.

Summary

Five experiments were conducted to directly test the precision hypothesis of the end-state comfort effect. The experiments revealed three core findings. First, grasps that increased the control over an object were preferred irrespective of the resulting arm postures. Second, the differences between the level of control that could be exerted with comfortable vs. uncomfortable arm postures are in principle large enough to elicit the end-state comfort effect outside the lab. Third, grasps that optimize control are frequently selected even when this implies adopting uncomfortable end-states. These three findings provide direct support that the end-state comfort effect emerges because it maximizes the control over the manipulated object at the end of object manipulations.

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Appendix A

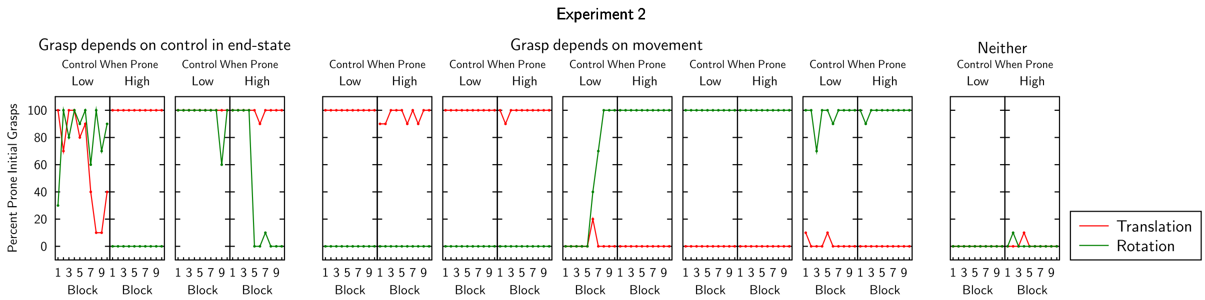
The following method was used to compute the virtual hand orientation from the real-world hand orientation. First, we computed the difference $\Delta\phi$ between the current real-world hand orientation ϕ_R and the real-world hand orientation associated with the maximum gain ϕ_G and recoded the value to the range between -180° to 180°, if necessary. Then the virtual hand orientation ϕ_V was computed:

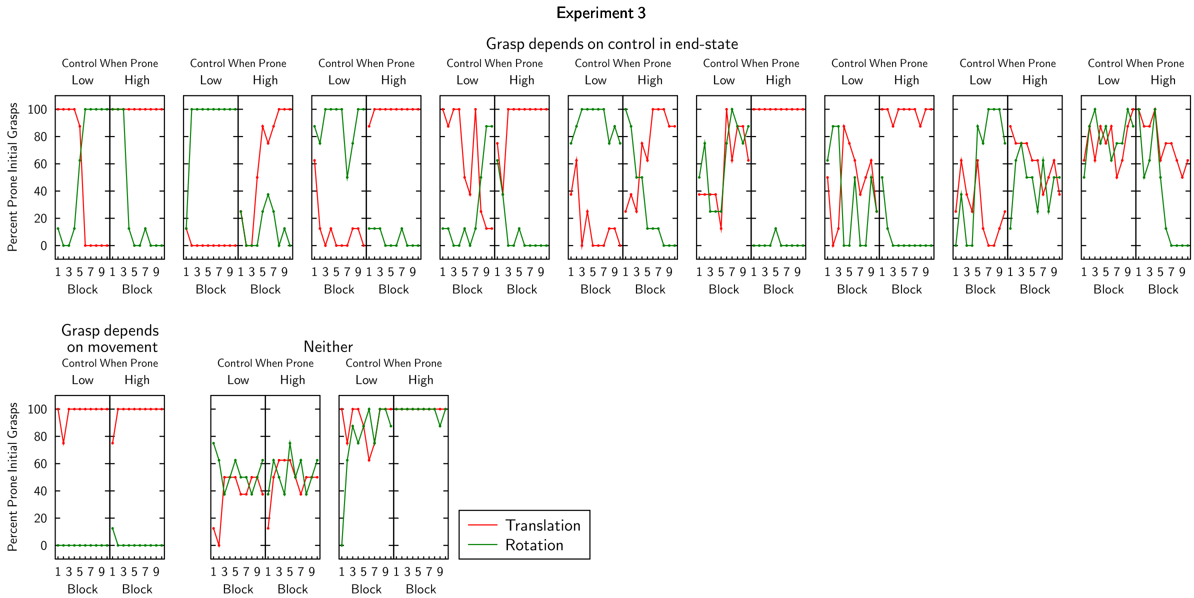
$$\phi_V = \begin{cases} -(180° + b)\dfrac{b}{\Delta\phi + b} + 180° + b + \phi_G, & \Delta\phi \geq 0 \\ -(180° + b)\dfrac{b}{\Delta\phi - b} - 180° - b + \phi_G, & \Delta\phi < 0 \end{cases}$$

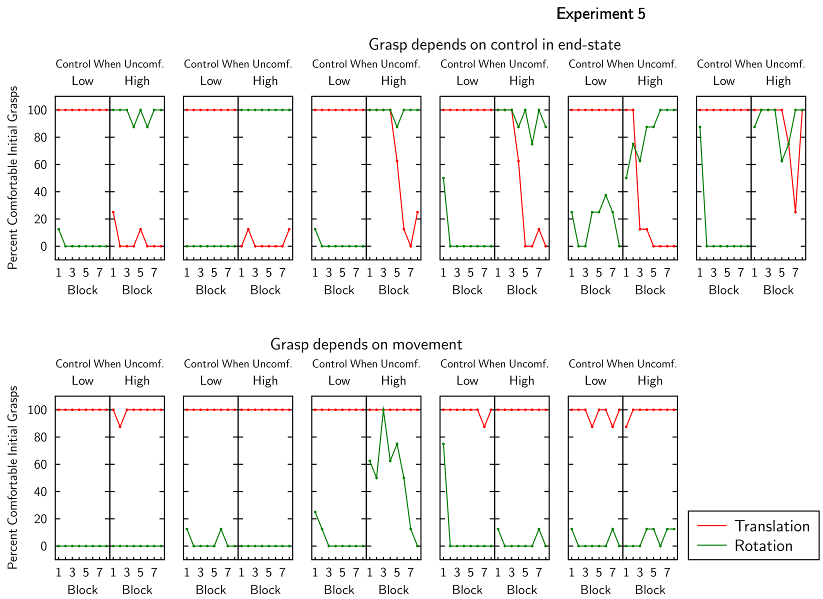
The coefficient *b* scales the values of the maximum and minimum gain and was set to 180°, resulting in gains between 0.5 and 2.0.

Electronic Supplement to: Precise movements in awkward postures: A direct test of the precision hypothesis of the end-state comfort effect

Oliver Herbort & Wilfried Kunde







The figures show the percentage of prone (Exp. 2, 3) or comfortable (Exp. 5) initial grasp as a function of movement, block, and gain manipulation for each participant. Participants are grouped in three categories (see main text), depending on whether grasps maximize control in the end-state, grasps depend on the object manipulation, or grasps neither maximize control nor depend on the movement.