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Illusion Effects on Grasping Are Temporally Constant Not Dynamic

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The authors tested whether the effects of the Ebbinghaus illusion on grasping are corrected during late phases of the movement. Surprisingly, the grasp aperture was corrected neither under no-vision ($N = 52$) nor under full-vision ($N = 48$) conditions. The authors show that previous reports of a correction (e.g., S. Glover & P. Dixon, 2002a) are due to 2 artifacts: (a) inclusion of time points at which the target object was already touched and (b) erroneous statistics. This removes the central evidence on which S. Glover and P. Dixon's (2001a) planning–control model of action is based. In addition, the authors' results can help to refine more classic notions of motor control (e.g., R. Woodworth, 1899). In consequence, the authors reject S. Glover and P. Dixon's (2001a) planning–control model but not classic online-control theories.

Keywords: planning–control, Ebbinghaus illusion, grasping

Glover and Dixon proposed that motor acts are guided by two different processes, an early planning process and a late control process (e.g., Glover, 2002, 2004; Glover & Dixon, 2001a, 2002a). They assumed that the early planning process is more "ventral" and therefore more closely related to perception, whereas the control process is more "dorsal" and relatively independent of perception. This view is different from the well-known view of Goodale and Milner (1992). Glover and Dixon (2001a, 2002a; Glover, 2002, 2004) assumed that the ventral cortical stream controls the first phase of the movement and the dorsal stream controls the final phase, whereas Milner and Goodale (1995) assumed that the whole movement is controlled by the dorsal cortical stream (Goodale & Milner, 2004).

The most important evidence Glover and Dixon presented for their planning–control model of action is the "dynamic illusion effect": the finding that contextual visual illusions (e.g., the Ebbinghaus–Titchener illusion) exert a much larger effect on early phases of a movement than on late phases (Glover & Dixon, 2001a, 2002a). Presuming that theses illusions are generated in the ventral (perceptual) stream, Glover and Dixon (2001a, 2002a) saw their finding as an indication that actions are first controlled by the ventral stream (planning) and later by the dorsal stream (control).

Glover and Dixon (2002a) found dynamic illusion effects independent of whether participants saw hand and stimuli during execution of the grasping movement or not (full-vision vs. no-vision conditions). We tested whether these effects really exist using improved methodology. On the basis of our results, we suggest that both effects, the dynamic illusion effects under full-vision as well as under no-vision conditions, as reported by Glover and Dixon (2002a), are due to artifacts. Because the theoretical implications of the existence or absence of dynamic illusion effects under full-vision and under no-vision conditions are very different, we will discuss these implications first.

Implications of a Dynamic Illusion Effect With Full Vision

The dynamic illusion effect under full-vision conditions would hardly be surprising and would therefore not constitute strong evidence for Glover and Dixon's (2001a) planning–control model. There is a long tradition of theories that assumes that the final phase of a movement can be corrected by visual feedback processes (e.g., Elliot, Binsted, & Heath, 1999; Jeannerod, 1988; Keele & Posner, 1968; Woodworth, 1899). Typically, early phases of a movement are assumed to be ballistic, whereas late phases are controlled by feedback loops. If a grasping movement is affected by a visual illusion, visual feedback mechanisms might be able to detect this deviation and correct for it.

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But this would only tell us that there are feedback mechanisms at work during the final phases of the movement. Classic motor control theories as well as Milner and Goodale's (1995) perception–action model allow for such feedback mechanisms. Therefore, the very specific assumptions of Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model about the role of the ventral and dorsal streams during movement execution would not gain much support from this finding. Milner and Goodale's (1995) perception–action model has another problem with this finding, because they assume that grasping is not deceived by contextual visual illusions at all. But, if there is an illusion effect, they would certainly allow for online corrections under full-vision conditions (cf. Goodale & Milner, 2004).

Online corrections have been shown in a number of studies. For example, Paulignan, Jeannerod, MacKenzie, and Marteniuk (1991) and Castiello, Bennett, and Stelmach (1993) presented grasp targets that unpredictably changed their size during execution of the movement. These studies found that the grasp aperture was quickly corrected to the new size of the target object (depending on the paradigm within 170 or 300 ms). Although this is a convincing demonstration of visual online-control processes, there are still some open questions that we can address when studying the temporal dynamics of visual illusions on grasping: (a) The perturbations were typically very large and salient (e.g., a disk changed in diameter from 4 cm to 7 cm in Jeannerod, 1981, or from 1.5 cm to 6.0 cm in Paulignan et al., 1991). Because errors induced by visual illusions are less salient (the target object never changes) and much smaller, they can help us to explore the sensitivity of these online corrections. (b) It is not entirely clear which information was used for the correction. Either the correction could result from a constant monitoring of the current finger position in relation to the attempted grasp points on the target, which would correspond to a feedback mechanism, or it could be induced by the change of the target object alone, which would correspond to a feed-forward mechanism. Illusion effects on grasping could help us to disentangle these two possibilities, because the target object is not changed. If the finger position is monitored relative to the target, then the bias introduced by the illusion should be detected and corrected at some time. If, on the other hand, only the target object is monitored, then the illusion effect should not be corrected because the target object never changes.

Implications of a Dynamic Illusion Effect Without Vision

Quite remarkably, Glover and Dixon (2002a) also found a dynamic illusion effect under no-vision conditions: Even if participants could not see hand and stimuli during movement execution, the illusion effect decreased at the end of the reach-to-grasp movement. This is a very surprising result. As long as the hand does not touch the target object, vision is the only source of information that could tell the motor system about the veridical size of the object. Therefore, classic online-control mechanisms cannot be responsible for this decrease of the illusion effect under no-vision conditions.

One possible explanation for this apparent paradox is the idea that the veridical information of the object's size is computed as long as the stimulus is visible, stored, and used during final phases of the movement to correct for the illusion effect. This is exactly the explanation proposed by Glover and Dixon's (2001a) planning–control model: They assumed that online control is performed by the control system, which processes visual information independent of and parallel to the perceptual system. Also, they assumed that the control system is not deceived by contextual illusions as the Ebbinghaus illusion and therefore computes and stores the veridical size of the target object. Finally, they assumed that the control system only affects late phases of the movement, whereas early phases are controlled by the perceptual (planning) system.

Accepting these assumptions, the dynamic illusion effect both under no-vision as well as under full-vision conditions can be explained. The planning system is deceived by the illusion and, because it controls early phases of the movement, leads to an illusion effect at the beginning of the grasp. The control system is not deceived by the illusion; it stores the veridical size, and when it controls the late phase of the movement, the illusion effect deteriorates.

Note that Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model resembles to some extent the perception–action model (Goodale & Milner, 1992; Milner & Goodale, 1995): Glover and Dixon's (2001a) planning system is similar to Milner and Goodale's (1995) perceptual system, and Glover and Dixon's (2001a) control system is similar to Milner and Goodale's action system. Also, some of the neuroanatomical and neuropsychological notions are similar (Glover, 2004). The new aspect of the planning–control model is the temporal succession of the two systems: According to Glover and Dixon (2001a), movements are first guided by the ventral planning system and then by the dorsal control system, whereas Milner and Goodale assumed that movements are mainly guided by the dorsal action system and not by the ventral perceptual system (for a more detailed discussion of the differences and similarities between the models, see Goodale & Milner, 2004).

In its emphasis on online-control processes, Glover and Dixon's (2001a) planning–control model is also similar to classic notions of online control (e.g., Elliot et al., 1999; Jeannerod, 1988; Keele & Posner, 1968; Woodworth, 1899). However, it differs from these notions in assuming that there are two separate representations of object size, one in the perceptual system and the other in the motor system. The motor representation is assumed to be calculated independently, to be veridical, and to be stored and used to correct the movement even under no-vision conditions. Also, the planning–control model differs from the more classic ideas about online control in its relatively strong inferences about underlying brain structures involved with motor control (e.g., Glover, 2004).

At first sight, the planning–control model seems to be superior to the perception–action model and to classic notions of online control: It can explain why there is an effect of contextual illusions on grasping and why this effect seems to be corrected during the movement even under no-vision conditions. However, this comes at a high theoretical cost. The model rests on a lot of assumptions, which are mainly based on the evidence the model is supposed to explain: the dynamic illusion effect under full-vision and no-vision conditions. To accept such a model, we should be very sure that the central evidence on which it is based (the dynamic illusion effect) really exists. Because only the dynamic illusion effect under no-vision conditions cannot be explained by classic online-control mechanisms, it seems beneficial to scrutinize the evidence for this effect first.

Taking a closer look at the data of Glover and Dixon (2002a) shows that there clearly seems to be a decrease of the illusion effect over time in the no-vision condition. In fact, the decrease is even larger than in the full-vision conditions (cf. Figure 5 in Glover & Dixon, 2002a). This is in itself a surprising and unexpected result. But what about replications of the effect? Only a few studies attempted to replicate Glover and Dixon's (2002a) dynamic illusion effect under no-vision conditions, typically with negative results (Danckert, Nadder, Haffenden, Schiff, & Goodale, 2002; Franz, 2003b).

Unfortunately, all of these studies had certain methodological limitations, as did have the original studies of Glover and Dixon (2002a). Therefore, we decided to test the dynamic illusion effect under no-vision as well as under full-vision conditions in a methodologically more rigorous way than has been done before. Before describing our results, we will first discuss the methodological concerns we had with the previous studies.

Methodological Problem 1: Touching the Target Object Can Contaminate the Measured Illusion Effects

When studying the dynamic illusion effect, we have to make sure that we do not include time points in the analysis when the fingers have already touched the target object. Obviously, when the object is grasped any illusion effect will be gone—because of the mechanical interaction of the fingers with the object. Therefore, if we want to isolate the illusion effect, we have to make sure that the analysis is not contaminated by including data in which the fingers already touched the target object.

The contamination can occur in two different ways, which both decrease the measured illusion effect and which are both effective as soon as only one finger touches the target object: (a) The target object could be larger than the motor system expects. In this case, one or both fingers will touch the target object earlier than expected. This will slow down the finger and lead to a larger aperture between the two fingers than was programmed by the motor system. The larger aperture will be more veridical, and this will artificially reduce the measured illusion effect. (b) The target object could be smaller in reality than the motor system expects. In this case, one or both fingers will touch the object later than expected, and the fingers will close more than was originally programmed by the motor system. Again, the aperture will be more veridical, and the measured illusion effect will be artificially reduced.

It is likely that times at which the fingers touched the target object were included in Glover and Dixon's (2002a) study, because the endpoint for inclusion in the analysis was defined as the time when the thumb stopped moving in a forward direction. To see this problem, try it yourself: Place an object in front of you, grasp it, and move it back to your body (as participants did in Glover & Dixon, 2002a). Watch for the time when the thumb no longer moves in a forward direction. Usually, you will have touched the object at this time. In consequence, it is well possible that part of the dynamic illusion effect found by Glover and Dixon (2002a) was due to this contamination at late time points. The problem is even more serious if we take into account that in Glover and Dixon's (2002a) study, a large proportion of the decrease occurred at very late time points, well beyond the time of the maximum grip aperture (MGA). (In other studies, Glover & Dixon, 2002b, used a slightly different end criterion, which was based on a threshold for the velocity of the thumb. In Experiment 2, we will show that this criterion can lead to the same problem).

Although it seems that the study of Glover and Dixon (2002a) used an end criterion that was too late, one might argue that the study of Franz (2003b) used an end criterion that was too early: Time points after the MGA were not included in the analysis. This was done because after the MGA, the fingers are already very close to the target object and quite often will touch it, which would contaminate the data. But given that Franz (2003b) did not find the dynamic illusion effect, this approach might have been too conservative: If Glover and Dixon's (2002a) online-control mechanism is mainly active after the MGA, then Franz (2003b) might simply have missed the dynamic illusion effect. To clarify these issues, we must analyze time points after the MGA, while ensuring that the fingers did not yet touch the target object. This was one of the main objectives of the present study.

Methodological Problem 2: Glover and Dixon (2002a) Predicted a Decrease Only for the Corrected Illusion Effects

The second methodological problem is related to the fact that—at first sight—the effects of visual illusions on grasping seem to increase (instead of decrease) early in a reach-to-grasp movement. This can be seen in Figure 1, which shows the results of Franz (2003b): Participants repeatedly grasped disks of different sizes, whereas perception of the size was distorted by two different levels of the Ebbinghaus illusion. The figure shows the grip aperture for different time points as a function of the illusion and the physical size of the target object. The illusion effect is the difference in grip aperture between the two curves (as shown in Figure 2a). Inspecting the figure shows that—at first sight—the illusion seems to increase instead of decrease, as suggested by Glover and Dixon (2002a).

However, this is not yet a contradiction to Glover and Dixon's (2002a) planning–control model, because at early time points the grip aperture hardly responds to any variation of size, even if the physical size is varied: The slopes of the linear functions that relate grip aperture to physical size are small at earlier time points (see Figure 2b). For an evaluation of the illusion effects, we have to take into account this weaker overall responsiveness. That is, we have to "correct" the illusion effects for the physical size effects. Only after this correction will we be able to detect a dynamic decrease of the illusion effect, as predicted by the planning–control model.

The correction is pretty simple: At each time point, we divided the illusion effect (see Figure 2a) by the slope (see Figure 2b). This results in corrected illusion effects (see Figure 2c). The figure shows that in the study of Franz (2003b) the corrected illusion effects were surprisingly constant and did not decrease, contrary to Glover and Dixon's (2002a) proposal.

Note that the correction is an integral part of Glover and Dixon's (2002a) argument (for a more detailed discussion of the logic of the correction, see Franz, 2003a; Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; and Glover & Dixon, 2001a). Only after the correction did they predict a dynamic decrease of the illusion

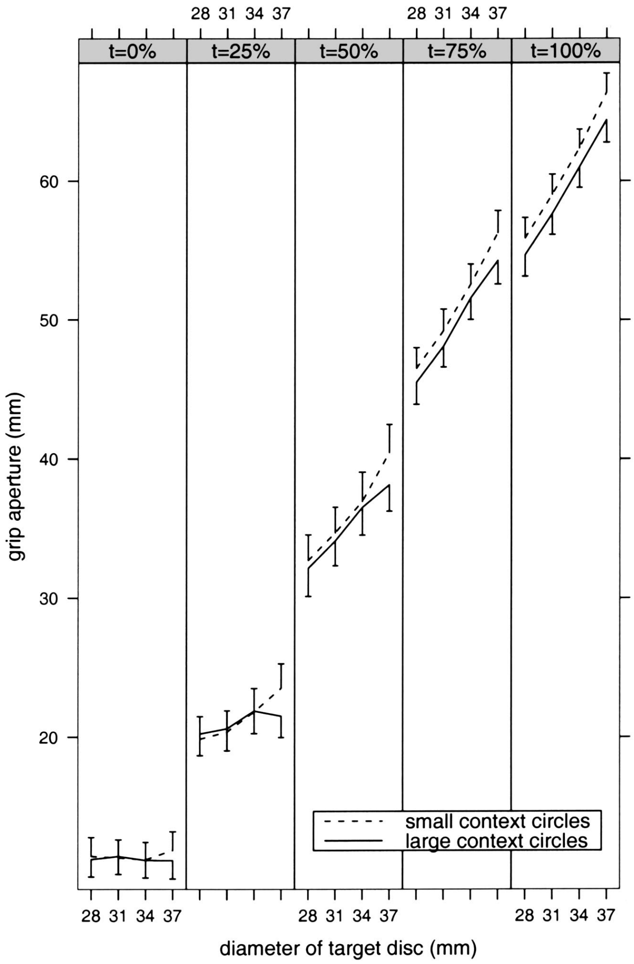

Figure 1. Grip aperture at different time points (t) of the reach-to-grasp movements in the study of Franz (2003b). The grip aperture is shown as a function of the physical size of the target disk (28, 31, 34, 37 mm), of the Ebbinghaus illusion (small vs. large context elements), and of time (time was normalized such that t = 0% corresponded to the start of the movement and t = 100% corresponded to the time of the maximum grip aperture). Error bars depict ±1 standard error of the mean.

effect (cf. Glover, 2004; Glover and Dixon, 2002a, used the phrase *scaled illusion effect* instead of *corrected illusion effect*).

This has important consequences for the interpretation of the study of Danckert et al. (2002). This study did not calculate corrected illusion effects for each time point and therefore cannot be seen as a test of the planning–control model of Glover and Dixon (2002a). (To be more specific, Danckert et al., 2002, did correct for the different slopes between grasping and the perceptual measure at time [t] = 100% of their time. But they did not correct for the different slopes, which are present in grasping at different time points—which is needed to test the existence of Glover and Dixon's, 2002a, dynamic illusion effect).

The correction leads to a further methodological issue because the corrected illusion effects are calculated as a ratio: At each time point, the illusion effect is divided by the slope. Calculating confidence limits for such a ratio, with variability in the numerator as well as in the denominator, is not trivial. Consider the case that the confidence limits of the denominator contained zero. In this case, we divide by numbers that can be arbitrarily close to zero, such that the corrected illusion effect can attain arbitrarily large positive or negative values (negative, if the denominator gets below zero). Exact confidence limits for such a ratio can be derived using a method that in statistics is called Fieller's theorem (Fieller, 1932, 1954; for a tutorial, see Franz, 2004a). Most important, the Fieller confidence limits will reach infinity if the denominator is too close to zero. Such data points with infinite confidence limits are not informative and should be discarded from further analyses.

This problem can arise at early phases of the movement, because here the slope (which is in the denominator) is very close to zero.

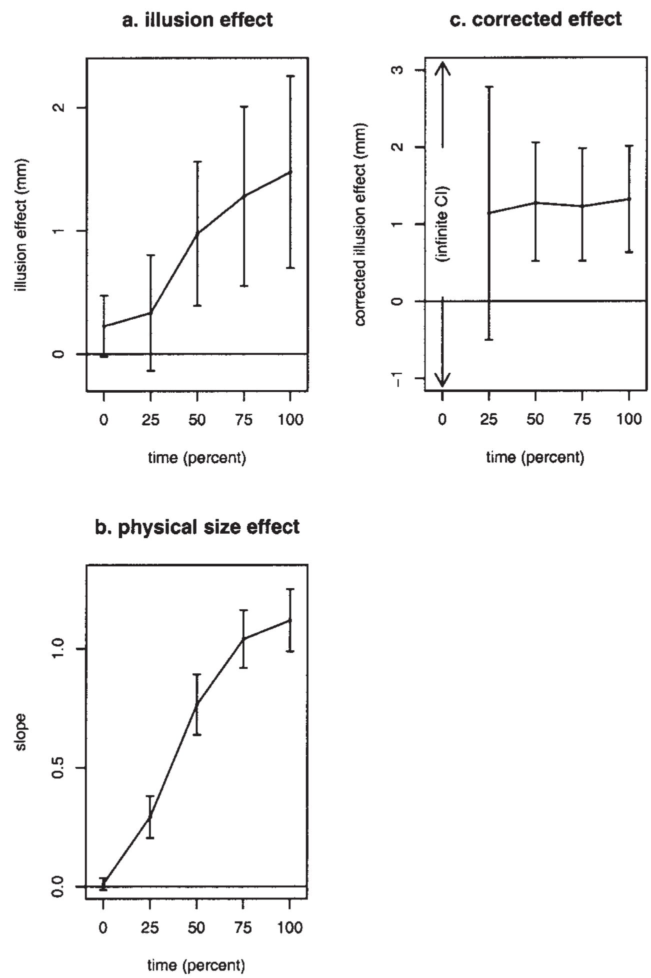

Figure 2. a: Effects of the Ebbinghaus illusion on grasping as a function of time for the data from Figure 1. The illusion effect is the mean difference in aperture when grasping one or the other version of the illusion. b: Effects of a physical variation of size on grasping. The physical size effect is the mean slope of the functions that relate grip aperture to physical size. c: Corrected illusion effects (i.e., illusion effects divided by physical size effects) and 95% confidence limits (CIs) as calculated by the mathematically exact method (Fieller, 1954; Franz, 2004a). The exact method gives infinite confidence limits at time = 0%, which leads to the exclusion of this data point. All error bars depict 95% confidence limits. From "Is There a Dynamic Illusion Effect in the Motor System?" by V. H. Franz, 2004b, *Behavioral and Brain Sciences, 27*, p. 35. Adapted with permission.

An example can be seen in Figure 2. At $t = 0\%$, the confidence limits of the slope contain zero (see Figure 2b). This leads to infinitely large confidence limits for the corrected illusion effect (see Figure 2c), such that we have to exclude this data point from the analysis.

None of the studies on the dynamic illusion effect calculated the exact Fieller confidence limits, including our own study (Franz, 2003b). For this study, we performed a recalculation that showed that the statistical method we originally used (the individual effects method) resulted for the given data in similar confidence limits as the exact Fieller method. These exact values are depicted in Figure 2c. The other studies (Glover & Dixon, 2001a, 2001b, 2002a, 2002b) used a method that implicitly assumes that the denominator has no variance. This zero-variance method can lead to large liberal deviations from the desired confidence level. In the next paragraph, we will sketch why the zero-variance method ignores the variance of the denominator, and in Experiment 2, we will demonstrate this problem. For a comprehensive discussion and comparison of the different methods, see Franz (2004a).

For the zero-variance method, one divides (separately for each time point) the individual illusion effect of each participant i ($i = 1 \ldots N$) by the overall slope (calculated across all participants):

$$\text{corrected}_i = \frac{\text{illusion}_i}{\text{slope}_{\text{overall}}}.$$

From these individual corrected effects, the mean and standard error are calculated. It is easy to show that this procedure is equivalent to simply dividing at each time point the mean illusion effect and its standard error by the overall slope, such that one gets for the mean corrected effect and its standard error:

$$\overline{\text{corrected}} = \frac{\overline{\text{illusion}}}{\text{slope}_{\text{overall}}}$$

$$SE_{\overline{\text{corrected}}} = \frac{SE_{\overline{\text{illusion}}}}{\text{slope}_{\text{overall}}}.$$

Inspecting the formulas shows that this procedure does not take into account the variability of the slope. Clearly, this is problematic. To justify this approach, we would have to assume that the measured slope corresponded to the "true" value of the slope in the population, such that the variability of the slope was zero. In consequence, the zero-variance approach will often underestimate the variability of the corrected illusion effect and therefore result in liberal statistical tests. As we will see in Experiment 2, this problem is most pronounced at early time points, when the slopes are still relatively close to zero.

To summarize, we identified the following potential methodological pitfalls: (a) We should not include parts of the trajectories at which the target object is already touched. (b) We must calculate the corrected illusion effects for each time point to be able to test Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model. (c) When calculating the corrected illusion effects, we should use the appropriate statistics.

Experiment 1: No Vision

We tested whether a dynamic illusion effect exists under no-vision conditions. This was done by reanalyzing a very large set of data from Franz, Bülthoff, and Fahle (2003). Special care was taken to analyze the trajectories as long as possible, excluding time points at which the participants had already touched the target object.

The data we used for our analysis have a number of advantages: (a) The sample size was very large: 52 participants took part in the study. This should provide us with ample statistical power to detect a dynamic illusion effect if it exists (the sample size is a factor of 3–8 larger than in other studies on this topic). (b) The Ebbinghaus illusion was presented as two pairs of Ebbinghaus figures (see Figures 3a and 3b). For each pair, the distance between the central target disk and the surrounding context circles was matched. This controls for possible artifacts on grasping, which might be caused by obstacle-avoidance behavior (as suggested by Haffenden, Schiff, & Goodale, 2001, and Danckert et al., 2002; but see the discussion in Franz et al., 2003). The control for obstacle avoidance comes, however, at the cost of reduced perceptual and motor effects of the Ebbinghaus illusion. This is one more reason for the large sample size we used.

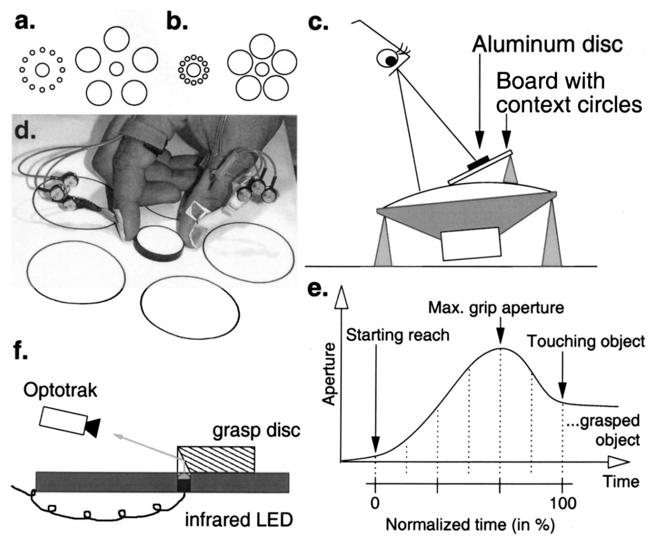

Figure 3. a and b: The Ebbinghaus illusion used in this study. A circle surrounded by larger circles is perceived as being smaller than if surrounded by smaller circles (and vice versa). In Experiment 1, we used four Ebbinghaus figures: two with the context elements being far from the central disk (a) and two with the context elements being near to the central disk (b). In Experiment 2, we used only the two far versions. Note that participants always saw only one of the Ebbinghaus figures at a time (see Franz et al., 2000, for a discussion of this issue). c: Apparatus. Participants viewed a board with the context circles drawn on it. In the center of the context circles, an aluminum disk was positioned. This disk was grasped by the participants. The monitor was only used in the perceptual task of Experiment 1 (which is of no interest here and is discussed in Franz et al., 2003). d: A participant grasping the aluminum disk. e: A prototypical grasp movement. Before the object is touched, the aperture between the index finger and the thumb reaches a maximum (Max.), which is larger than the size of the object. f: Apparatus used in Experiment 2 for the touch-locked end criterion. One Optotrak marker was placed below the grasp disk such that it illuminated a small reflecting area at the side of the grasp disk. The Optotrak measured the mirror image of the marker. The grasp disk moved as soon as the fingers touched it, and this movement was detected as velocity signal in the mirror image of the marker. LED = light-emitting diode.

If Glover and Dixon's planning–control model of action is correct (Glover, 2002, 2004; Glover & Dixon, 2001a, 2002a), then we should find a dynamic illusion effect. That is, the corrected illusion effects should decrease before the grasp object is touched.

Method

The setup of this experiment was already described in Franz et al. (2003). For clarity of presentation, the relevant points are repeated here and, where necessary, described in more depth than in Franz et al. (2003).

Participants. Fifty-two volunteers (29 women and 23 men) participated in the experiment, ranging in age from 16 to 47 years (M = 25.4 years). In return for their participation, they were paid DM15 per hour (approximately €7.50 or $7.50). Participants had normal or corrected-to-normal vision (Snellen equivalent of 20/25 or better; Ferris, Kassoff, Bresnick, & Bailey, 1982), normal stereopsis of 60 s of arc or better (Stereotest circles, Stereo Optical, Chicago, IL), and were right handed (Oldfield, 1971). Written, informed consent was obtained from the participants prior to their inclusion in the study, and the rights of the participants were protected according to the 1964 Declaration of Helsinki.

Stimuli. The four variants of the Ebbinghaus figure used in our experiment are shown in Figures 3a and b. The Ebbinghaus figures were presented sequentially, such that in each trial the participants saw only one of the four figures. The large (vs. small) context circles were 58 mm (vs. 10 mm) in diameter. In the near (vs. far) condition, the distance between the midpoint of the target disk and the nearest point on the context circles was 24 mm (vs. 31 mm). All context circles were drawn on a board. The targets were aluminum disks 31, 34, or 37 mm in diameter (corresponding to 2.7, 3.0, and 3.3 degrees of visual angle, respectively) and 5 mm in height. To maximize the similarity between the three-dimensional target disk and the two-dimensional context circles, we minimized shadows and had participants view the stimuli from above.

Apparatus. Participants sat on a stool and used a chin rest to keep the position of the head constant. They looked down at a 21-in. monitor (effective screen diagonal of 48.5 cm) as if looking at the top of a table (see Figure 3c). The monitor was positioned at a distance of approximately 65 cm from the eyes. The screen of the monitor served as a table for the presentation of the stimuli (the monitor was needed for the perceptual task, which is not relevant for the current investigation). The screen was tilted to be oriented perpendicular to gaze direction. Participants wore liquid crystal (LC) shutter glasses (Milgram, 1987), which allowed us to efficiently suppress vision. The grasp trajectories were recorded using an Optotrak system (Northern Digital Incorporation, Waterloo, Ontario, Canada; sampling rate = 100 Hz): Six infrared light-emitting diodes were mounted on two little flags (three light-emitting diodes per flag). The flags were attached to the thumb and index finger (cf. Figure 3d). Before the start of the experiment, we determined the typical grasp points on the fingers, and we measured them relative to the markers on the flags. This enabled us to calculate the trajectories of the grasp points and to determine for each grasp the grip aperture as a function of time.

Procedure. Participants grasped the target disk with their dominant right hand, lifted the disk, and deposited it at the right side of the monitor. After this task, the experimenter returned the target disk and prepared the next trial. The LC shutter glasses suppressed vision as soon as the grip started, such that participants could neither see their hand nor the stimulus during grasping. Participants had 4 s to finish the movement (from opening of the shutter glasses until depositing the disk). If the time limit was exceeded, the trial was repeated at a randomly determined later time. Trials were presented in a computer generated, (pseudo) random order. Each participant performed 72 grasps (3 sizes of the central disk × 4 illusion conditions × 6 repetitions).

Participants also performed a perceptual task in which we determined the perceptual effect of the Ebbinghaus illusion. For the present investigation, the perceptual task is not relevant and will therefore not be described here. For further details, see Franz et al. (2003).

Before each trial, the experimenter selected the current combination of context circles and target disk, positioned the target disk on top of the board with the context circles, and mounted the board on top of the monitor. The LC shutter glasses were opaque during this preparation. When finished, the experimenter pressed a button to open the LC shutter glasses and to start the trial. The order of tasks was counterbalanced among participants, such that 26 participants performed the perceptual task first, and the other 26 participants performed the motor task first.

Data Analysis

For each grasp, time was normalized relative to movement onset (t = 0%) and to an end criterion (t = 100%; cf. Figure 3e), which ensured that the fingers did not yet touch the target object. The validity of our criteria for movement onset, MGA, and for the endpoint were assessed by inspecting a large number of trials, as shown in Figure 4.

Movement onset was defined as the first moment at which the thumb or index finger had moved more than 2 cm away from the resting position. MGA was defined as the maximum aperture between onset of the movement and the time when the participants had moved the target disk by more than 2 cm.

The endpoint was defined as the first minimum of the index finger or the thumb in z direction (height above the board on which the target disk was mounted) within a region of 10-cm radius around the target disk. If at this time the aperture between the thumb and index finger was already smaller than the disk size plus a safety margin of 2 mm, then the algorithm selected the latest time at which the aperture was still larger than this safety margin. This criterion proved to be more reliable than a criterion based solely on the aperture between the index finger and thumb. One reason is that the positioning of the target disk varied slightly between trials (it had to be put in place by the experimenter for each trial). Another reason is that participants typically first touched the surface of the board on which the disk was mounted before lifting the disk.

Figure 4 shows some example trajectories for which our criteria were applied in top and side views. It can be seen that our criteria worked well for relatively smooth movements (see Figures 4a and b) as well as for movements in which participants "searched" for the target disk in the final phase of the movement (see Figures 4c and d). The endpoint for inclusion in the analyses is not too early (which would result in a loss of data) but also not too late (which would result in a contamination of the trajectories from touching the target disk). Reaction time was defined as the time from opening of the LC goggles until movement onset. Movement time was defined as the time from movement onset until the end criterion.

For each time point, the illusion effect and the mean slope of the linear functions, which related the grip aperture to physical size, were calculated. This was done by fitting at each time point a linear mixed effects model (Pinheiro & Bates, 2002) with the factors size of target disk (31, 34, and 37 mm) and illusion context (small–near, large–near, small–far, and large–far context circles). Illusion effects were determined as the contrasts large–near versus small–near and large–far versus small–far. From these values, the corrected illusion effect was calculated by dividing the illusion effect by the slope. We calculated 95% confidence limits for this ratio according to Fieller's theorem (Fieller, 1932, 1954), as described in the introduction and in detail by Franz (2004a).

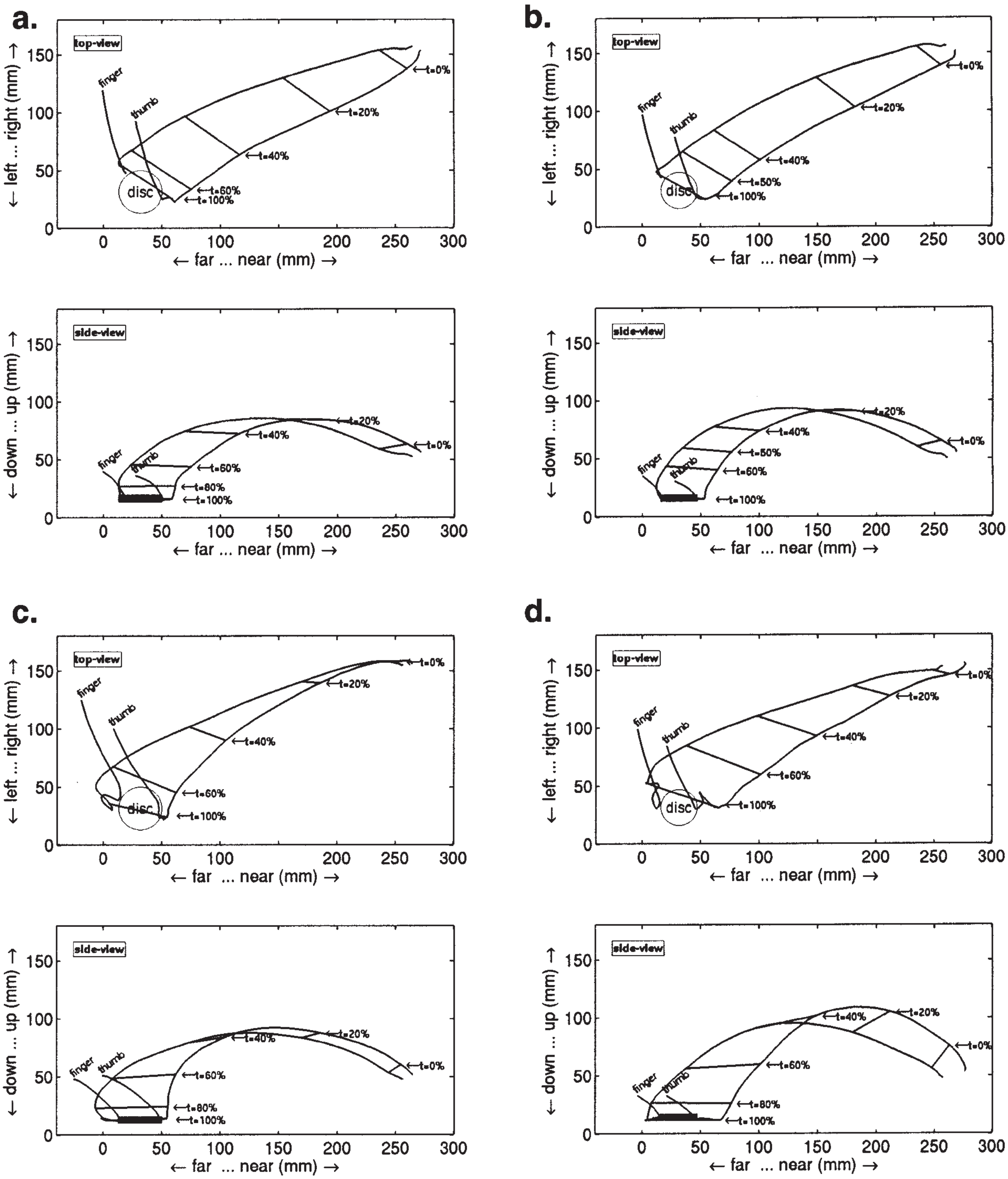

Figure 4. Example trajectories of four grasps in Experiment 1. Each grasp is seen from a top view and from a side view. The axis-labels *left . . . right*, *far . . . near*, and *down . . . up* are relative to the participant who was sitting at a position right of the panels. One can see that the criteria used in Experiment 1 work well for relatively smooth movements (a and b) as well as for movements in which participants "searched" for the target disc in the final phase of the movement (c and d): The endpoint for inclusion in the analyses is not too early (which would result in a loss of data) but also not too late (which would result in a contamination of the trajectories from touching the target disc). For further details, see the *Method* section of Experiment 1. t = time.

We used a significance level of $\alpha = .05$ for all statistical analyses. The p values above .001 are given as exact values. Parameter values are denoted by $X \pm Y$, with X being the mean and Y the standard error of the mean (*SEM*).

Results

The effect of the Ebbinghaus illusion on grasping was statistically significant. A repeated measures analysis of variance (ANOVA) on MGA, with size of target disk (31, 34, and 37 mm) and illusion context (small–near, large–near, small–far, and large–far context circles) as factors, revealed a highly significant main effect of the illusion, $F(3, 153) = 17.7$, $p < .001$, and of physical size, $F(2, 102) = 97.5$, $p < .001$, whereas the interaction between these factors was not significant, $F(6, 306) = 0.3$, $p = .94$. The pattern of the illusion effects for the grasping task across the four different illusion conditions was identical to the pattern found in perception. This aspect of the data is discussed in detail by Franz et al. (2003) and will not be considered here. In this article, we will focus on the temporal dynamics of the illusion effects in grasping.

The following variables are related to the time normalization. Movement onset was on average 856 ± 47 ms after stimulus presentation (i.e., opening of the goggles). MGA was on average at 515 ± 16 ms after movement onset, and the end criterion was reached at 671 ± 17 ms after movement onset. This corresponds to an average occurrence of the MGA at 76% of movement time, a result that fits well to the results found in other studies (typically, the MGA appears at about 75% of movement time; cf. Jeannerod, 1984; Smeets & Brenner, 1999).

Figure 5 shows the unfolding of grip aperture over normalized time for one of the illusion conditions (near-context circles; the

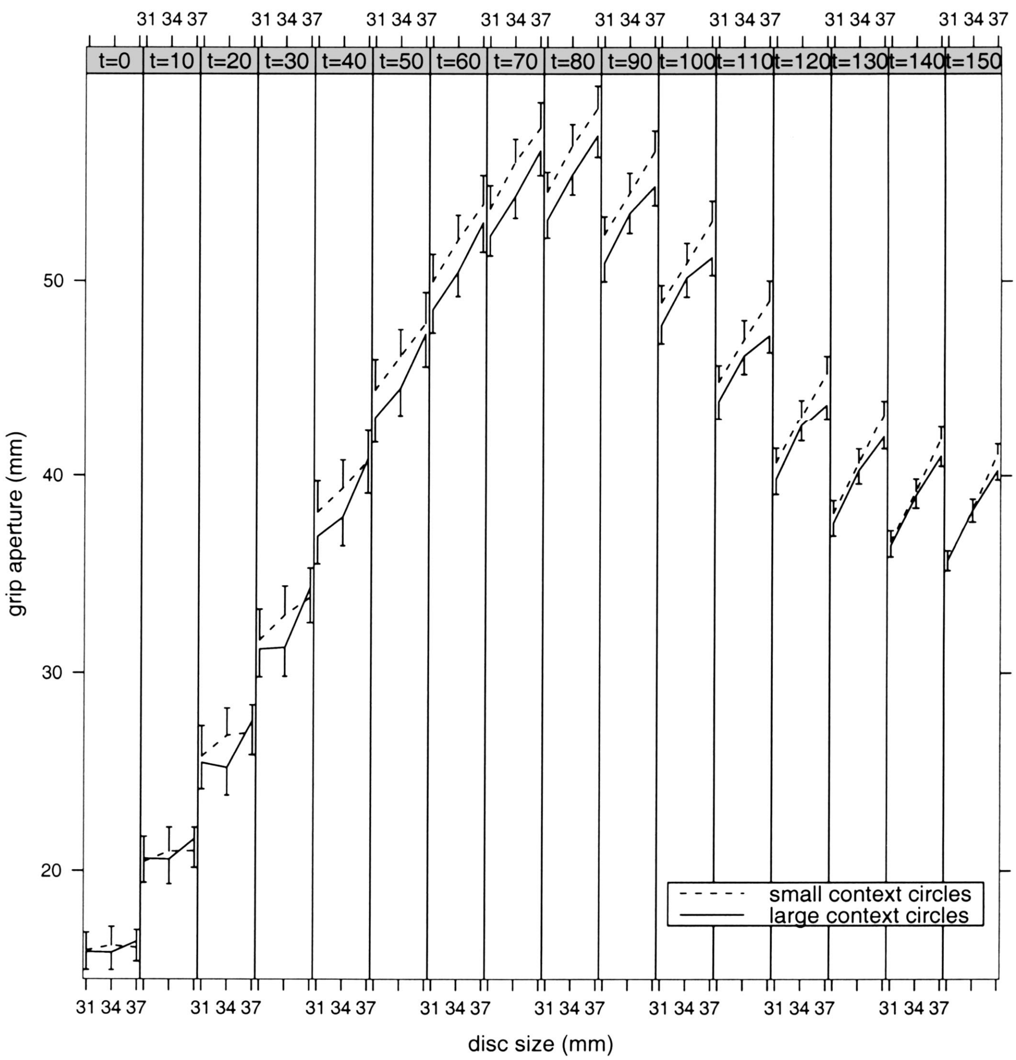

Figure 5. Grip aperture at different time points (t) of the reach-to-grasp movements for the near-context version of the Ebbinghaus illusion in Experiment 1. (Results for the far-context version were similar and are therefore not shown here). The illusion effects (i.e., the distances between solid and dashed lines) build up over time and then decay at later time points, when the participants grasp the target object. Error bars depict ±1 standard error of the mean.

graph for the far-context circles is very similar). The figure shows that the illusion effects (the distances between the dashed and the solid lines) built up over time until the time of the MGA. Also, the responsiveness to a physical variation of size (the slopes of the lines) increased during this time interval. Finally, at very late time points the illusion effect vanished, because here the participants had already grasped the target object.

Figure 6a shows the mean illusion effects for each of the illusion conditions, and Figure 6b shows the mean slopes, pooled across all illusion conditions. (This was done because the slopes constitute the denominator of the corrected illusion effects and variability in the denominator is problematic. Because the slopes were similar among the illusion conditions, we were able to pool the slopes to keep the variability as small as possible).

The corrected illusion effects are shown in Figure 6c. They were calculated by dividing at each time point the illusion effects (see Figure 6a) by the slope (see Figure 6b), and calculating the 95% confidence limits according to Fieller's theorem.

At early time points, the confidence limits for the corrected illusion effects are very large, because here the slopes (the denominators) are relatively close to zero. From about $t = 20\%$ on, the confidence limits for the corrected illusion effects are small

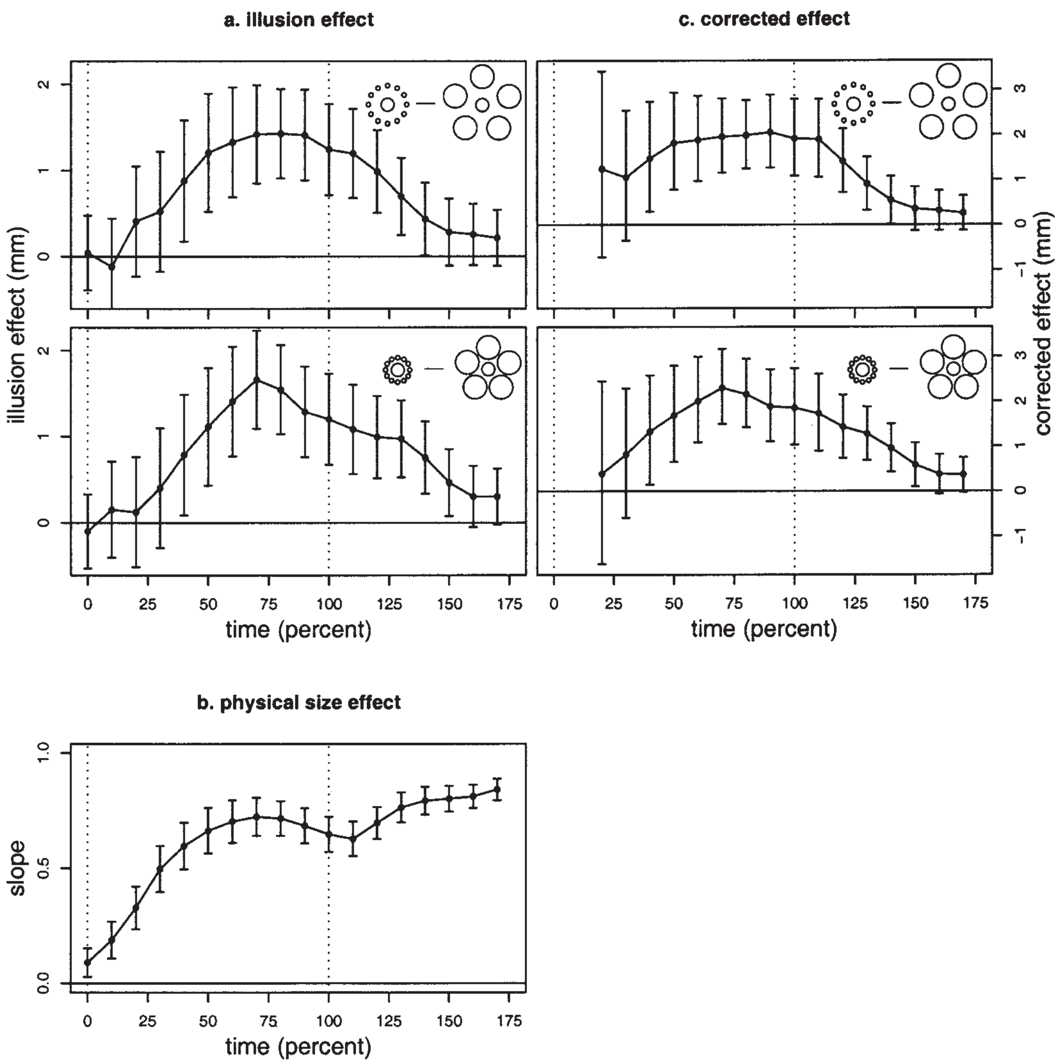

Figure 6. Illusion effects and corrected illusion effects in Experiment 1. a: Illusion effects as function of time for the two different versions of the Ebbinghaus illusion (the upper panel refers to the far-context version of the illusion; the lower panel refers to the near-context version). b: Mean slopes of the functions that relate grip aperture to physical size at each time point. c: Corrected illusion effects (the upper panel refers to the far-context version of the illusion; the lower panel refers to the near-context version). For each time point, the illusion effect is divided by the slope, and 95% confidence limits are calculated according to Fieller's theorem (Fieller, 1954; Franz, 2004a). At times before 20%, confidence limits were so large that these points are not shown. At times after 100%, participants had touched the target object. This leads to a trivial decrease of the measured illusion effect, which is due to the mechanical interaction of the fingers with the target. Error bars depict 95% confidence limits.

enough to be interpreted (the earliest time points analyzed by Glover and Dixon, 2002a, 2002b, were between 25% and 40%). Our data show no indication of a decrease of the corrected illusion effects up to our end criterion (t = 100%). Recall that our end criterion was chosen such that participants were likely to have not yet touched the target object (but will soon be touching it). After the end criterion, from about t = 110% on, the corrected illusion effects deteriorated. This is what can be expected simply because of the mechanical interaction when the fingers touch the target object.

In short, under no-vision conditions the corrected illusion effects are quite constant until the target object is touched. Even with our very large sample size, we did not find any indication of a dynamic decrease of the corrected illusion effects before the time of touch, as suggested by Glover and Dixon (2002a).

Discussion

Investigating the temporal dynamics of the Ebbinghaus illusion on grasping under no-vision conditions, we found remarkably constant corrected illusion effects over time (see Figure 6c). Our data show no indication that the corrected illusion effects decrease during no-vision grasp movements. This finding extends and replicates an earlier study (Franz, 2003b) and is in contrast to the findings of Glover and Dixon (2001a, 2002a) and to their planning–control model of action (Glover, 2002, 2004).

A further investigation of our data shows an additional intriguing phenomenon: The slopes that relate physical size to grip aperture show a local minimum at about t = 110% (see Figure 6b). The slopes first increase from t = 0% up to the time of the MGA (t = 76%); then they decrease until t = 110%, and after this time they increase again. We interpret this local minimum as an independent marker of the time when the target object is touched. To get an idea of this phenomenon, imagine we would remove the target object at the beginning of the movement and the hand would simply open and close (symmetrically in time). In this case, the slopes will first rise up to the maximal slope at the time of the MGA. Then, the hand will close again and the slope will fall to zero again. Now imagine what happens if the hand performs the same movement but we insert the target object during the closing phase. In this case, the fingers will "bump" into the target object and, consequently, the slope will rise again to a slope of one at the time when the object is grasped. The time of this bump is exactly the local minimum in the slope function—and therefore an indication when the target object is touched.

The occurrence of the local minimum is independent of our end criterion, such that we can use the local minimum to evaluate and improve our end criterion. In addition, the mere existence of the local minimum argues for the fact that we used an end criterion that was quite well locked to the time of touching. The local minimum would have washed out had we chosen an end criterion that is not locked to touching.

Comparing the time of the local minimum (t = 110%) with the time of our end criterion (t = 100%) shows that our end criterion was quite well defined—slightly too early, though. But even when considering the corrected illusion effects up to the time of the local minimum, the corrected illusion effects remain constant. In fact, the corrected illusion effects start to deteriorate right at the time when the local minimum occurs. This provides strong evidence against the dynamic illusion effect, as conceived by Glover and Dixon (2002a), because it shows that the corrected illusion effects only change when we see an effect of touching the target object on the slopes (and not before).

How can we explain the different outcome of the present study in comparison with the study of Glover and Dixon (2002a)? In the introduction, we discussed methodological problems that could have caused the discrepant results. Most important, Glover and Dixon (2002a) probably underestimated the illusion effects in late phases of the movement, because it is likely that in their studies time points were included at which participants had already touched the target object. In addition, Glover and Dixon (2002a) might have overestimated the accuracy of their results in early phases of the movement, because they did not calculate the exact Fieller confidence limits for the corrected illusion effect. Underestimating the size of the confidence limits at these early time points could strengthen the false impression of a decrease of the corrected illusion effect over time.

Therefore, we think our results pose serious problems to the model proposed by Glover and Dixon (2001a, 2002a; Glover, 2002, 2004). The new aspect of their model is the notion that the control system is much more complex than has been traditionally assumed by theories of motor control. Most notably, they assumed that the control system creates its own internal representation of object size, parallel to and independent of the perceptual system. This motor representation is assumed to be refractory to the Ebbinghaus illusion, such that the veridical size can be stored until it is used in late phases of the movement to control and correct the action. Because of this stored veridical representation of object size, Glover and Dixon (2001a, 2002a; Glover, 2002, 2004) could explain a decrease of the illusion effect on grasping in no-vision conditions (which traditional motor control approaches cannot explain). According to our results, however, there is no dynamic decrease of the illusion effect on grasping in no-vision conditions. Consequently, we do not need the complex model proposed by Glover and Dixon (2001a, 2002a; Glover, 2002, 2004).

There is one further issue: If our conclusion is correct and there is no dynamic illusion effect on grasping in no-vision conditions and if the dynamic illusion effect Glover and Dixon (2002a) found in these conditions is due to artifacts, what about the dynamic illusion effect Glover and Dixon (2002a) found in full-vision grasping? Our results do not necessarily imply that there is no dynamic illusion effect in these conditions. For example, grasping is more accurate under full-vision conditions, such that the end criterion Glover and Dixon (2002a) used (i.e., the time when the thumb ceased to move in a forward direction) could be locked more precisely to the time of the touch.

To clarify these questions, we conducted another large experiment under full-vision conditions. When designing this new experiment, we also took the opportunity to further improve our methodology: (a) We developed a device that allows us to directly measure when the target object starts to move—thereby measuring the time of touch more directly (cf. Figure 3f and the *Method* section for Experiment 2). (b) We changed the grasp task in such a way that participants moved the target object in their midsagittal plane (they "fetched" the object to their body). Because this is the response used by Glover and Dixon (2002a), we were now able to directly evaluate the response criteria used by Glover and Dixon (2002a, 2002b) and to compare them with our precise, touch-locked end criterion. This can provide further insight into whether the dynamic illusion effects found by Glover and Dixon (2002a) were due to artifacts caused by including time points at which the hand had already touched the target object.

Experiment 2: Full Vision

In this experiment, we investigated whether there is a dynamic illusion effect when participants had full vision of hand and stimuli during grasping. Also, we improved the methodology such that we were able to measure directly when the participants touched the grasp object. Therefore, we were able to better exclude artifacts that arise from the fingers touching the target object. Finally, we arranged the responses of the participants in such a way that we could directly compare the different end criteria used by Glover and Dixon (2002a, 2002b) with our touch-locked end criterion.

Method

The apparatus of this experiment was functionally almost identical to the apparatus used in Experiment 1. However, the experiments were performed in different laboratories (Experiment 1: Max Planck Institute for Biological Cybernetics, Tübingen, Germany; Experiment 2: University of Giessen, Giessen, Germany) such that minor differences occurred. All important differences are described in the following paragraphs.

Participants. Forty-eight volunteers, most of them students of the University of Giessen (33 women and 15 men) participated in the experiment, ranging in age from 18 to 51 years ($M = 25$ years). In return for their participation, the students received course credit. Participants had normal or corrected-to-normal vision and were right handed. The rights of the participants were protected according to the 1964 Declaration of Helsinki.

Stimuli. Two variants of the Ebbinghaus figure that were identical to the far conditions in Experiment 1 were used in this experiment (see Figure 3a). The targets were aluminum disks 32, 34, or 36 mm in diameter (corresponding to 2.8, 3.0, and 3.2 degrees of visual angle, respectively) and 5 mm in height.

Apparatus and procedure. The new apparatus at the University of Giessen was designed in such a way that it was possible to measure the exact time of touching the grasp disk with high precision. For this procedure, one Optotrak marker was placed below the grasp disk such that it illuminated a small reflecting area at the side of the grasp disk (see Figure 3f). The Optotrak was positioned such that it tracked the mirror image of the marker. As soon as the fingers touched the grasp disk, the disk moved, and this movement was detected as a velocity signal for the mirror image of the marker. Because the grasp disks are very lightweight, they exert only little inertia forces (the masses of the disks were 12, 13, and 14 g). Therefore, this setup is very precise in detecting the first touch of the grasp disk.

In order to be maximally comparable with the procedures of Glover and Dixon (2002a), we changed the direction of the grasp movements relative to Experiment 1. Although in Experiment 1 participants moved the grasp disk to the side, they now moved it back to their body. This enabled us to use for comparison the same end criterion that Glover and Dixon (2002a) had used—the time when the thumb stops to move in a forward direction (GD–zero-velocity criterion)—and the end criterion that Glover and Dixon (2002b) had used—the time when the velocity of the thumb falls below a certain criterion (GD–slow-velocity criterion; see *Data Analysis* section).

Participants grasped the target disk with their dominant right hand. They had 3 s to finish the movement (from opening of the shutter glasses until depositing the disk). Each participant performed 72 grasps (3 sizes of the central disk × 2 illusion conditions × 12 repetitions).

As in Experiment 1, participants also performed a perceptual task. This was done as a control for the perceptual effect. In this task, participants viewed the same stimuli as in the grasping task for 3 s. During this time they selected a circle from a graded series to indicate the perceived size of the target disk. The graded series consisted of circles (smallest diameter = 28 mm; largest diameter = 40 mm; step size = 0.5 mm) printed on a board that was placed symmetrically in front of the participants (distance to the eyes = 42 cm). The participant selected the circle by pointing at it, and the experimenter recorded its size (the size of the circles was written at the side of the board such that only the experimenter could read it). Each participant performed 24 judgments (3 sizes of the central disk × 2 illusion conditions × 4 repetitions). The succession of perceptual and grasping tasks was counterbalanced between participants.

Data Analysis

As in Experiment 1, time was normalized relative to movement onset ($t = 0\%$) and to the end criterion ($t = 100\%$). To be as comparable as possible with the studies of Glover and Dixon (2002a, 2002b), we defined movement onset as the first time at which the velocity of the finger or thumb exceeded a value of 10 cm/s. Glover and Dixon (2002a) used a criterion of 10 cm/s for the thumb velocity, and Glover and Dixon (2002b) used a criterion of 2.5 cm/s for the thumb velocity. Note that using a slightly different criterion would only marginally change the results because the onset of the movement is fairly unambiguous.

For the end criterion, we used a touch-locked criterion. For this we used the mirror image of the marker, which was placed below the grasp disk (see Figure 3f and the *Apparatus and procedure* section). Touch of the grasp object was defined as the first time at which the velocity of this mirror image exceeded a value of 1 cm/s and at which at least one of the fingers was closer than 40 mm to the grasp object. Because at this time the target object was already touched, we had to go backwards in time to define our end criterion. We did this by calculating a velocity baseline for the mirror image from the start of the recording until the time of touch and then went back from the time of touch until the velocity of the mirror image reached baseline level for the first time again.

In addition, we also applied the end criteria used by Glover and Dixon (2002a, 2002b) to our data. These were (a) the GD–zero-velocity criterion, as defined by Glover and Dixon (2002a), and (b) the GD–slow-velocity criterion, as defined by Glover and Dixon (2002b). For the GD–zero-velocity criterion, the end criterion for the time normalization "was set at the time when the thumb ceased to move in a forward direction" (Glover and Dixon (2002a, p. 269). That is, the first time after movement onset when the velocity component of the thumb in "forward" direction is zero (S. Glover, personal communication, October 14, 2003). For the GD–slow-velocity criterion, the end criterion is the time when the thumb velocity is for the first time after movement onset below 2.5 cm/s. In most studies, Glover and Dixon used the GD–slow-velocity criterion (Glover & Dixon, 2002b; Glover, Rosenbaum, Graham, & Dixon, 2004) and only in the study on the Ebbinghaus illusion (Glover & Dixon, 2002a) the GD–zero-velocity criterion. Therefore, we decided to evaluate the validity of both criteria.

Reaction time was defined as the time from opening of the LC goggles until movement start. Movement time was defined as the time from movement start until the end criterion. Trials for which the reaction times fell outside the interval (100; 800) or the movement times fell outside the interval (250; 1,200) were excluded from further analyses (all values in milliseconds). This resulted in an exclusion of 2.5% of the 3,456 trials for the touch-locked criterion, 3.2% for the GD–zero-velocity criterion, and 7.1% for the GD–slow-velocity criterion. Note that the exclusion criteria are similar to those used by Glover and Dixon, who used the reaction time intervals (250; 1,500) and (50; 800) and the movement time intervals (250; 1,500) and (250; 1,000), which resulted in the exclusion of 3.4% and 7.5% of the trials (values are for Glover & Dixon, 2002a, and Glover & Dixon, 2002b, respectively).

For a comparison of the statistical methods used by Glover and Dixon (2002a, 2002b) with the mathematically exact Fieller method, we calculated 95% confidence limits for the corrected illusion effects at early time points according to the Fieller method and according to Glover and Dixon's (2002a, 2002b) method (the zero-variance method, as described in the introduction). For this procedure, we simulated the situation in the studies of Glover and Dixon (2002a) and Glover and Dixon (2002b) by using the means and *SEM*s of Experiment 2 with the GD–zero-velocity criterion and the GD–slow-velocity criterion, respectively. Because Glover and Dixon (2002a, 2002b) used much smaller sample sizes (we used a sample size of $N = 48$ participants, whereas Glover & Dixon, 2002a, used $N = 11$; and Glover & Dixon, 2002b, used $N = 6$), we estimated the variability of these studies by scaling the *SEM*s by the appropriate factors ($\sqrt{\frac{48}{11}}$ and $\sqrt{\frac{48}{6}}$).

Results and Discussion

The effect of the Ebbinghaus illusion on grasping was statistically reliable: A repeated measures ANOVA on MGA, with size of target disk (32, 34, and 36 mm) and illusion context (small vs. large context circles) as factors, revealed a highly significant main effect of the illusion, $F(1, 47) = 10.8$, $p = .002$, and of physical size, $F(2, 94) = 184.3$, $p < .001$, whereas the interaction between these factors was not significant, $F(2, 94) = 1.3$, $p = .28$. Similarly, the Ebbinghaus illusion affected perception: A repeated measures ANOVA on the perceptual measure, with size of target disk (32, 34, and 36 mm) and illusion context (small vs. large context circles) as factors, revealed a highly significant main effect of the illusion, $F(1, 47) = 38.6$, $p < .001$, and of physical size, $F(2, 94) = 262.8$, $p < .001$, whereas the interaction between these factors was not significant, $F(2, 94) = 0.04$, $p = .97$. As in previous studies (Franz, 2003a; Franz et al., 2003; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999), the average illusion effect on MGA (0.59 ± 0.18 mm) and the illusion effect on perception (0.96 ± 0.16 mm) were not significantly different, $t(47) = 1.6$, $p = .12$. For a comprehensive discussion, see Franz (2001). Here, we will focus on the temporal dynamics of the illusion effects in grasping.

Movement onset was on average 364 ± 11 ms after stimulus presentation (i.e., opening of the goggles). MGA was on average 552 ± 14 ms after movement onset, and the touch-locked criterion was reached 710 ± 15 ms after movement onset. This corresponds to an average occurrence of the MGA at 78% of movement time. As in Experiment 1, these results are in accordance with the results found in other studies.

Figure 7 shows the unfolding of grip aperture over normalized time. The pattern of results is very similar to Experiment 1. Figure 8a shows the mean illusion effects, and Figure 8b shows the mean slopes as functions of normalized time. The corrected illusion effects are shown in Figure 8c. As in Experiment 1, they were calculated by dividing at each time point the illusion effect (see Figure 8a) by the slope (see Figure 8b), and calculating the 95% confidence limits according to Fieller's theorem.

Two things can be seen in Figure 8: (a) The corrected illusion effects are remarkably constant over time. Only around the time of touch ($t = 100\%$) does the corrected illusion effects start to decrease. This result replicates the results of Experiment 1 under full-vision conditions with a more precise end criterion to determine the time of touch. (b) The slopes show (as in Experiment 1) the characteristic local minimum at the time of touch. This is consistent with the interpretation of the local minimum in Experiment 1 as a second, independent marker of the time of touch: Right before touching the target object, the physical size effect (i.e., slope) decreases—and increases again after the fingers touched the target object.

A closer inspection of Figure 8 reveals that the local minimum in the slopes is a bit earlier than our touch-locked criterion (the minimum is at around $t = 95\%$, with 5% corresponding to 35 ms). That is, we see in the slopes the effect of touching the target object slightly earlier than in the touch-locked criterion. This might be a consequence of the touch-locked criterion being defined using the movement of the target object, which can lead to this small delay in the criterion (because the object must be touched to move; see the *Data Analysis* sections for methods we used to minimize this problem). This delay might also explain why there is a small decrease in the corrected illusion effect between $t = 95\%$ and $t = 100\%$. At these times, we already see the effects of touching the target object in the slopes (i.e., the slopes increase again); therefore, it is no surprise that we also see the effects of touching the target object in the corrected illusion effects (i.e., a small decrease). Note that this decrease between $t = 95\%$ and $t = 100\%$ is much smaller than the decrease found in the studies of Glover and Dixon (2002a, 2002b; see the next two sections, where we replicate the dynamic illusion effects found by Glover and Dixon, 2002a).

In short, even under full-vision conditions the corrected illusion effects are remarkably constant until the target object is touched. Even with our very large sample size, we did not find any indication of a dynamic decrease of the corrected illusion effect before the time of touch, as suggested by Glover and Dixon (2001a, 2002a; Glover, 2002, 2004).

Testing Glover and Dixon's (2002a, 2002b) end criteria. We set up this experiment such that we were able to apply the end criteria used by Glover and Dixon (2002a, 2002b) and to compare the outcome with the results we obtained with our touch-locked criterion.

The GD–zero-velocity criterion was reached 823 ± 12 ms after movement onset, and the GD–slow-velocity criterion was reached 789 ± 11 ms after movement onset. That is, both end criteria of Glover and Dixon (2002a, 2002b) were reached later than the touch-locked criterion (by 112 ± 6 ms and 78 ± 8 ms, respectively; cf. Figure 8a.; the GD–zero-velocity criterion is marked with a *Z* and the GD–slow-velocity criterion is marked with an *S*).

At these times, the target disk had moved already and therefore must have been touched by the fingers. This decreases the corrected illusion effects for two reasons: (a) Because of the mechanical interactions of the fingers with the grasp object, the illusion effect will be reduced. (b) Also because of the mechanical inter-

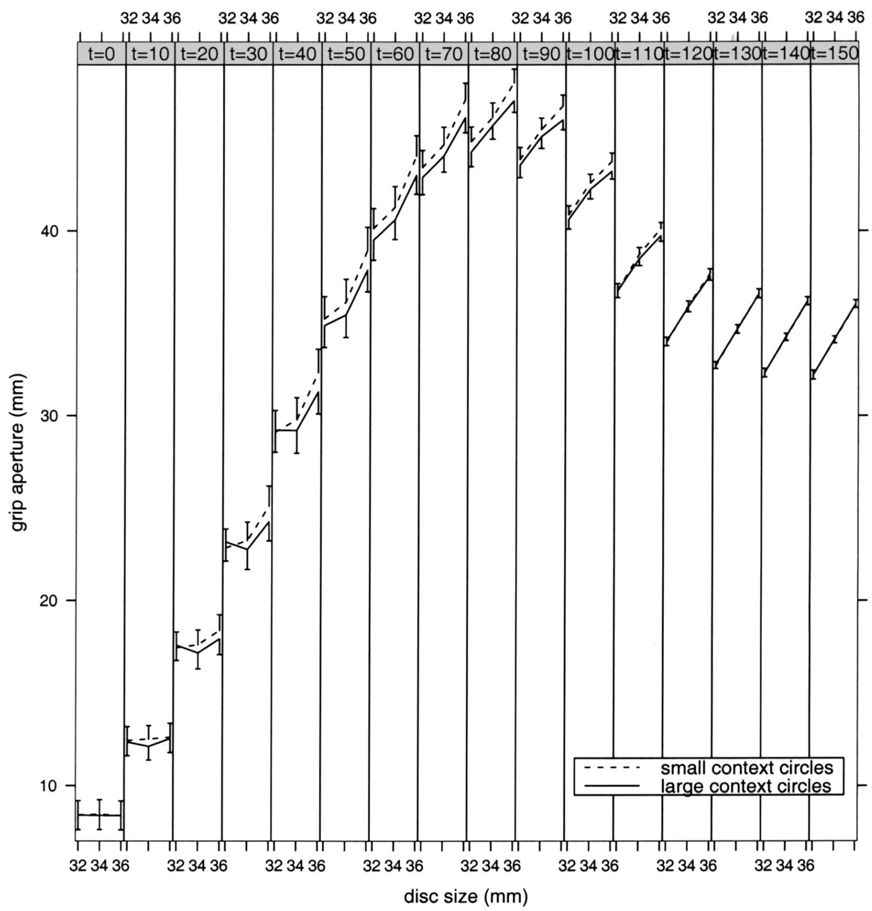

Figure 7. Grip aperture at different time points (t) of the reach-to-grasp movements in Experiment 2 using our touch-locked end criterion for the time normalization. The illusion effects (i.e., the distances between solid and dashed lines) build up over time and decay at later time points, when the participants grasp the target object. Error bars depict ±1 standard error of the mean.

actions of the fingers with the grasp object, the physical size effect will be increased (see Figure 8b). Both effects multiply in the calculation of the corrected illusion effect (because the numerator gets smaller and the denominator gets larger). Therefore, the corrected illusion effect is quickly reduced after touching the target object. This is what can be seen in Figure 8c.

We can go even further and investigate what would have happened had we used Glover and Dixon's (2002a, 2002b) end criteria for the time normalization. Can we reproduce the dynamic illusion effect of Glover and Dixon (2002a, 2002b) by simply exchanging our touch-locked criterion with one of their end criteria? Figure 9 shows the results for the GD–zero-velocity criterion, and Figure 10 shows the results for the GD–slow-velocity criterion. Indeed, these results are already very similar to the results reported by Glover and Dixon (2002a, 2002b). The corrected illusion effects decrease well before the end criteria and much more drastically than with the precise touch-locked criterion.

In summary, with the end criteria used by Glover and Dixon (2002a, 2002b), the target object had already been touched. If we apply their end criteria to our data, we can replicate the dynamic illusion effects found by Glover and Dixon (e.g., Glover & Dixon, 2002a, 2002b). However, these dynamic illusion effects are artifactual, because they are due to the mechanical interaction of the fingers with the target object and are not due to neuronal control mechanisms.

Testing Glover and Dixon's (2002a, 2002b) confidence intervals. In the introduction, we identified another problem of the methods used by Glover and Dixon (2002a, 2002b). Because the corrected illusion effect is calculated as a ratio (i.e., at each time point the illusion effect is divided by the slope), we have to be very careful when the denominator is close to zero. We argued that the statistics used by Glover and Dixon (2002a, 2002b) can underestimate the variability of the corrected illusion effects. In this section, we investigate how serious this problem is for typical grasping data.

We calculated 95% confidence limits for the corrected illusion effects at early time points. Here the problem is most pronounced because the slopes (i.e., the denominators) are close to zero. We applied Glover and Dixon's (2002a, 2002b) statistical method as well as the mathematically exact Fieller method to our data. To simulate the situation in the studies of Glover and Dixon (2002a, 2002b), we used the corresponding end criteria for the time nor-

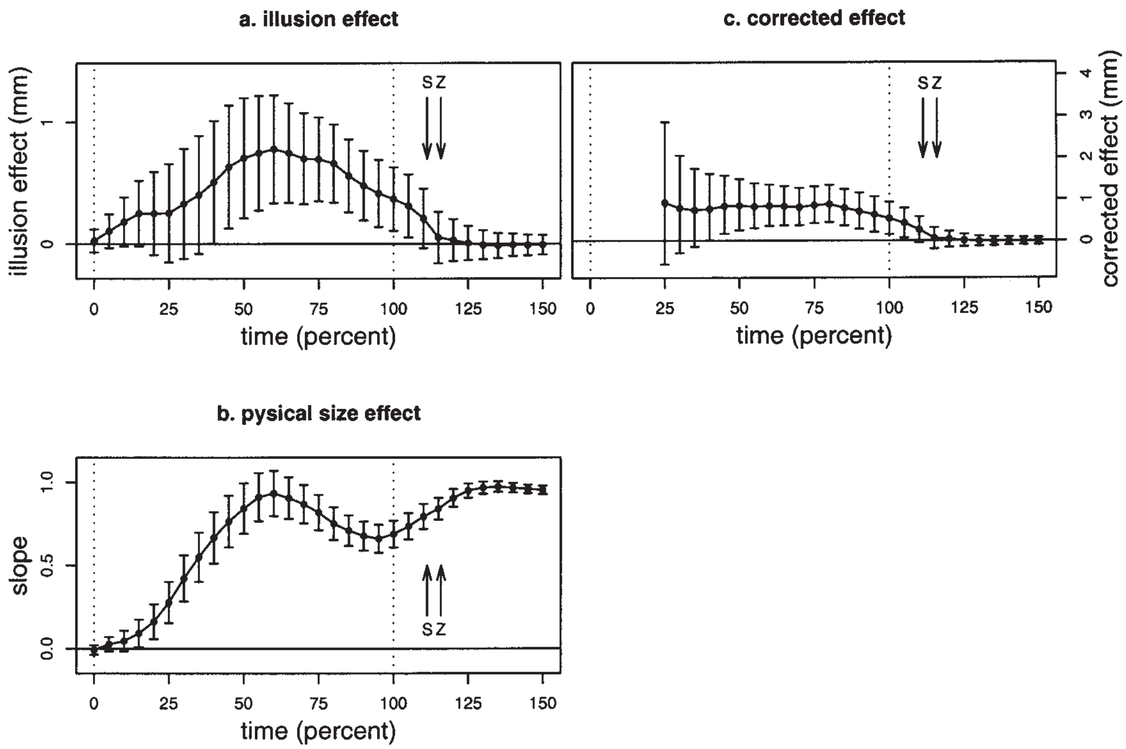

Figure 8. Corrected illusion effects in Experiment 2 using our touch-locked end criterion for the time normalization. a: Illusion effect at each time point. b: Mean slopes of the functions that relate grip aperture to physical size at each time point. c: Corrected illusion effects. For each time point, the illusion effect is divided by the slope, and 95% confidence limits are calculated according to Fieller's theorem (Fieller, 1954; Franz, 2004a). At times before 25%, confidence limits were so large that these points are not shown. At times after 100%, participants had already touched the target object. This leads to a trivial decrease of the measured illusion effect, which is due to the mechanical interaction of the fingers with the target. The arrows indicate the times of Glover and Dixon's (2002a, 2002b) end criteria: *Z* indicates their zero-velocity criterion, and *S* indicates their slow-velocity criterion. Both criteria are met after touching the target object. Error bars depict 95% confidence limits.

malization and estimated the variability of these studies, which was considerably larger than in Experiment 2 because much smaller sample sizes were used (cf. the *Data Analysis* section).

The results can be seen in Figure 11. Glover and Dixon's (2002a, 2002b) zero-variance method (solid error bars) led to remarkably smaller confidence limits than the mathematically exact Fieller method (dashed error bars; note that the exact Fieller method can lead to infinite confidence limits.). The underestimation is most pronounced in Figure 11b, which simulates a situation similar to the study of Glover and Dixon (2002b). Up to $t = 40\%$, Glover and Dixon's (2002a, 2002b) method leads erroneously to much smaller confidence limits than the exact method. This is problematic because Glover and Dixon (2002b) calculated and interpreted corrected illusion effects at times as early as $t = 25\%$. (Note that Glover & Dixon, 2002b, used in this study an illusion other than the Ebbinghaus illusion. However, for our comparison this does not make a major difference, because the critical factor is the size of the slope—which will be very similar between the studies).

If we inspect Figure 11 further, we can learn two more important properties of the corrected illusion effects. First, the corrected illusion effects become much more variable at early time points. This is a consequence of the denominator getting closer to zero. Here small variations of the denominator lead to huge deviations in the corrected illusion effects. To get an idea of this outcome, consider the simple case that the true corrected illusion effect was: $1 = \frac{0.1}{0.1}$. Now assume we made a small error in measuring the denominator, such that we obtained 0.001 instead of 0.1. This will result in a corrected illusion effect of 100. With a little more error, we will obtain a value of -0.001, which will result in a corrected illusion effect of -100. This is the reason why it is difficult to estimate the corrected illusion effects at early time points (and why we used unusually large sample sizes in our experiments; this reduces the variability of the denominator and therefore increases the time range at which we are able to estimate the corrected illusion effects with reasonable variability).

Second, there is a natural tendency for the corrected illusion effects to attain very large values if the denominator is positive but small. This is so because a measurement error that decreases the denominator has a larger impact on the corrected illusion effect than a measurement error that increases the denominator. Consider

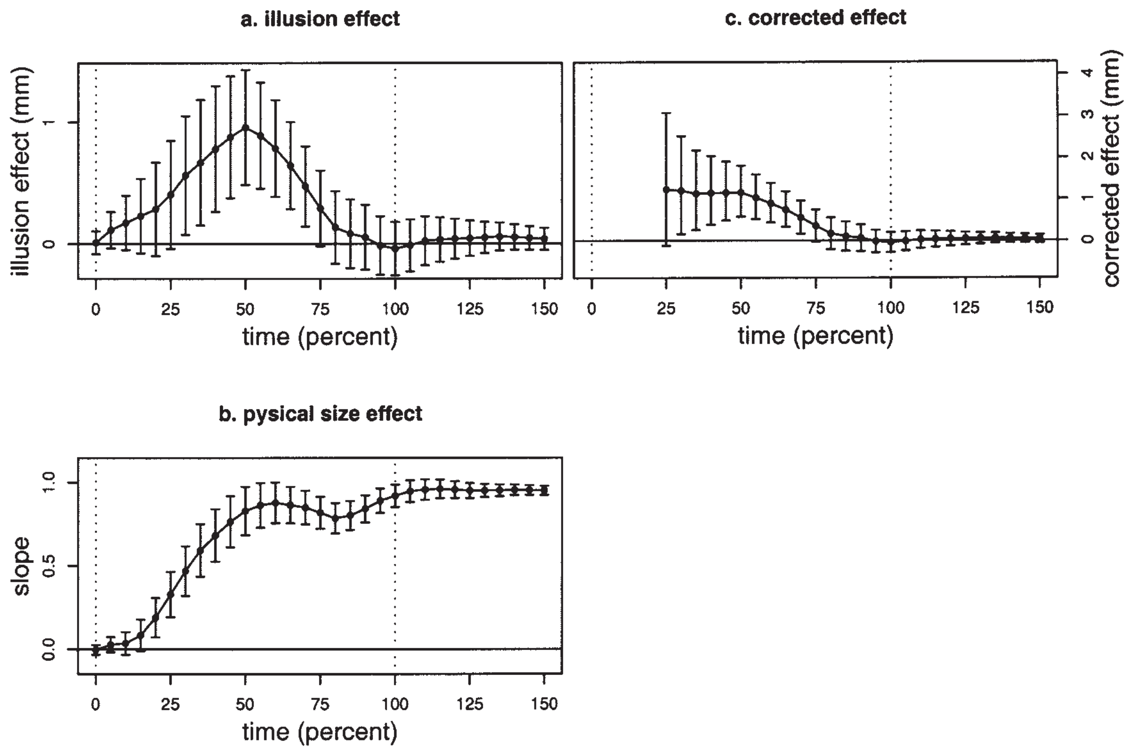

Figure 9. Corrected illusion effects in Experiment 2 using the Glover and Dixon zero-velocity criterion (Glover & Dixon, 2002a) for the time normalization. The end criterion was defined as the time when the thumb stopped to move in a forward direction. Participants already had touched the target object at the time of this end criterion. This leads to a trivial decrease of the corrected illusion effect. a: Illusion effects. b: Slopes. c: Corrected illusion effects. Error bars depict 95% Fieller confidence limits.

again our example of a true corrected illusion effect of $1 = \frac{0.1}{0.1}$. If we had two measurements, one with an error of +0.09 and the other with an error of –0.09, we would obtain corrected illusion effects of $10 = \frac{0.1}{0.1 - 0.09} = \frac{0.1}{0.01}$ and $0.53 = \frac{0.1}{0.1 + 0.09} = \frac{0.1}{0.19}$. Clearly, the first result looks much more impressive than the second result—despite both being because of the same amount of measurement error and the true value of the corrected illusion effect being 1 in both cases. Intuitively, we would guess that the true value should be roughly the mean of the two measurements: $5.265 = \frac{10 + 0.53}{2}$, but this is a misjudgment.

This statistical illusion of large corrected illusion effects is a simple consequence of the nonlinearity of the function $y = \frac{1}{x}$. If we use the mathematically exact Fieller statistics, we will be warned about this possibility by asymmetric confidence limits (an example for such an asymmetric confidence limit can be seen at $t = 25\%$ in Figure 11a). Glover and Dixon's (2002a, 2002b) zero-variance method underestimates the size of the confidence limits and cannot result in asymmetric confidence limits and therefore cannot warn us about this possibility.

In summary, corrected illusion effects can lead to wrong conclusions if the denominator is relatively close to zero and if we do not use the mathematically exact statistics. This will often result in an overestimation of the corrected illusion effects. The problem is most likely to occur at early time points, right at the times where Glover and Dixon (2002a, 2002b) found the largest corrected illusion effects.

General Discussion

Using improved methodology, we tested whether there exists a dynamic illusion effect when grasping the Ebbinghaus illusion. That is, we tested whether the corrected illusion effects decrease during movement execution. Up to the time of touch, we found remarkably constant effects of the illusion during all phases of the grasp movement. This was independent of whether vision of hand and stimuli was suppressed (see Figure 6c) or allowed (see Figure 8c) during movement execution. This finding is consistent with earlier findings that tested the movement only up to the time of the MGA (see Franz, 2003b, and Figure 2c).

We were able to replicate previous reports of a dynamic illusion effect (Glover & Dixon, 2001a, 2002a, 2002b) simply by including time points in the analyses at which the fingers already touched the target object (see Figures 9c and 10c), as was done in these studies. However, these time points should not be included because when touching the target object, the mechanical interaction of the fingers with the target object leads to a trivial decrease of the corrected illusion effect, which is not related to neuronal control mechanisms. In addition, we showed that the statistics used in Glover and Dixon's (2002a, 2002b) studies can seriously underestimate the variability at early time points (see Figure 11) and therefore reinforce the wrong impression of a dynamic illusion effect.

A short graphic summary of these results is given in Figure 12. Figure 12a shows our results for Experiment 2: no dynamic illusion effect. If we use one of Glover and Dixon's (2002a, 2002b)

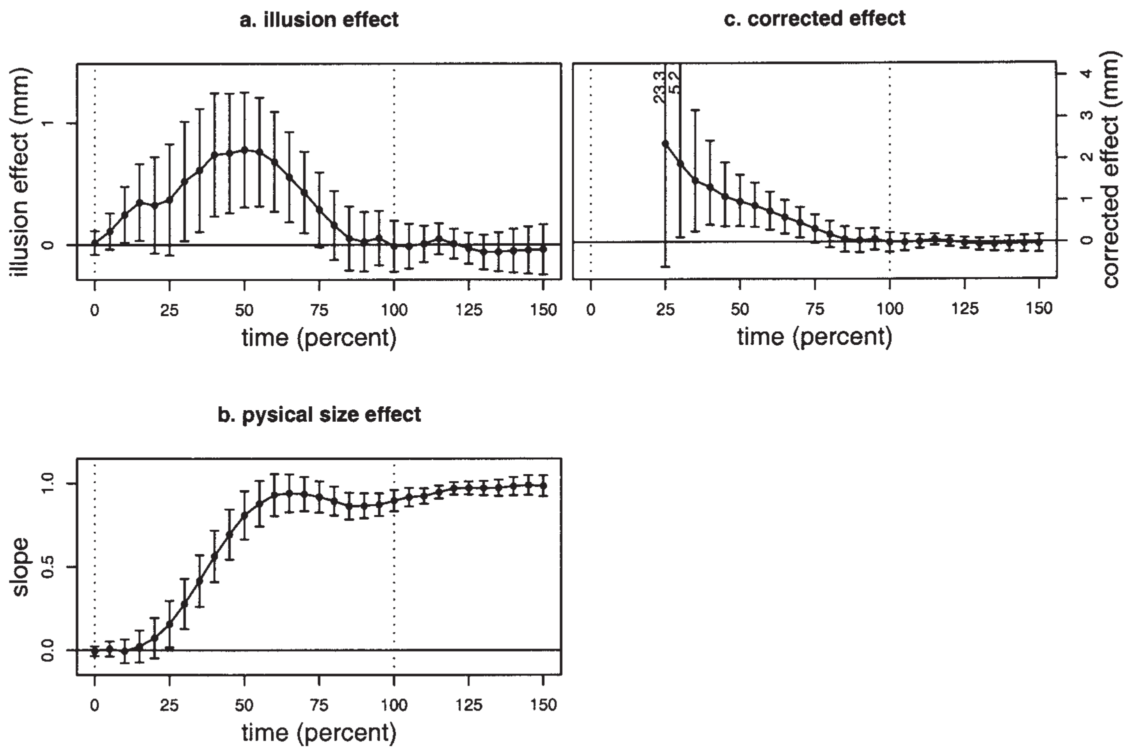

Figure 10. Corrected illusion effects in Experiment 2 using the Glover and Dixon slow-velocity criterion (Glover & Dixon, 2002b) for the time normalization. The end criterion was defined as the time when the velocity of the thumb fell below 2.5 cm/s. Participants already had touched the target object at the time of this end criterion. This leads to a trivial decrease of the corrected illusion effects. a: Illusion effects. b: Slopes. c: Corrected illusion effects. Vertical numbers (23.3 and 5.2) represent upper confidence limits, which are beyond the scale of the figure. Error bars depict 95% Fieller confidence limits.

end criteria (see Figure 12b) and their statistical method (see Figure 12c), then we get a dynamic illusion effect. For better comparison with the studies of Glover and Dixon (2002a, 2002b), we also show error bars depicting the *SEM*s instead of 95% confidence intervals (see Figure 12d). Comparing Figure 12d with the results of Glover and Dixon (e.g., Figure 5 in Glover & Dixon, 2002a, or Figure 2 in Glover & Dixon, 2002b) shows that this seems to be a clear replication of the dynamic illusion effect—but it is artifactual.

We therefore conclude that the dynamic illusion effects, as reported by Glover and Dixon (2002a, 2002b), are artifactual. This interpretation is also strengthened by the fact that Glover and Dixon (2002a) found the largest decrease in no-vision conditions, a finding that would be very surprising and hard to explain with neuronal control mechanisms—even in Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control framework.

If our interpretation is correct and there is no dynamic illusion effect, what are the consequences for the different models of motor control? In the introduction, we showed that the central evidence for Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model of action is the dynamic illusion effect under no-vision conditions. Only because of this effect were they justified in assuming a second independent system that computes the veridical size of the target object, stores it, and uses this stored information in final phases of the movement to correct for the effects of the visual illusion (even if vision of hand and stimuli is not possible at this time anymore). Given our results, we think it is safe to reject this model. This conclusion is supported by studies that used different experimental paradigms and also came to a negative appraisal of Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model (Handlovsky, Hansen, Lee, & Elliott, 2004; Meegan et al., 2004).

It is interesting to note that we also found that the corrected illusion effects did not decrease even if full vision of hand and stimuli were allowed during movement execution. How can this finding be related to more classic notions of motor control? Would these theories not predict that feedback mechanisms correct for the illusion late in the movement if vision is allowed? Classically, the question of feedback mechanisms in the grasp aperture has been studied using perturbation paradigms: The grasp target unpredictably changed its size during execution of the movement. It was found that the grasp aperture adapted quickly to this change (e.g., Castiello et al., 1993; Paulignan et al., 1991). Typically, this result has been interpreted as implicating that the grasp aperture is controlled by visual feedback mechanisms that permanently monitor the actual grasp aperture relative to the grasp object. We think that these findings can be reconciled with our findings in two different ways.

First, the error introduced by the illusion might be too small to trigger online corrections. The error could simply be below the

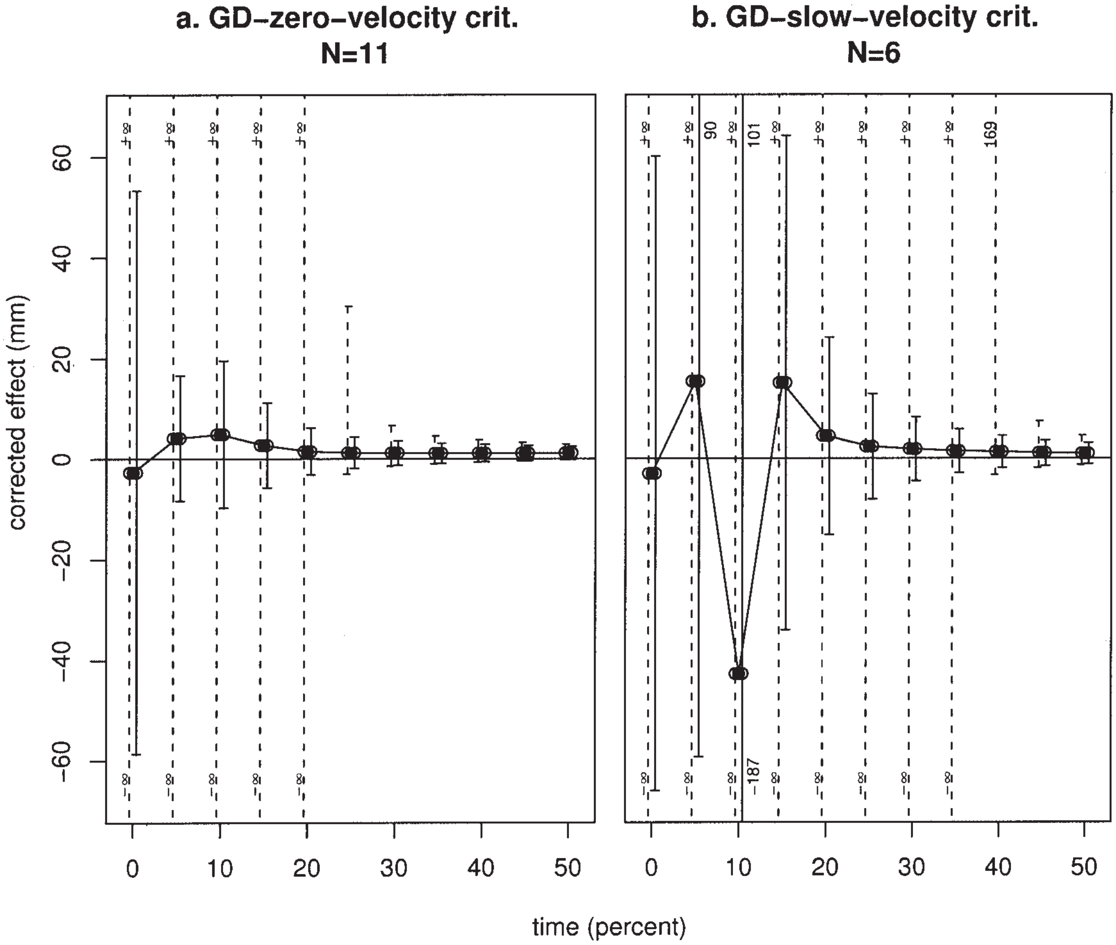

Figure 11. Comparison of Glover and Dixon's (GD) statistical method and the exact Fieller method. Using the data from Experiment 2, we simulated the situation in the studies of Glover and Dixon (2002a; Panel a) and Glover and Dixon (2002b; Panel b). We calculated confidence limits for the corrected illusion effects according to Glover and Dixon's (2002a, 2002b) method (solid error bars) and according to the mathematically exact Fieller method (dashed error bars). Only early time points are shown because here Glover and Dixon's (2002a, 2002b) method is most problematic. Vertical numbers represent upper or lower confidence limits, which are beyond the scale of the figure. crit. = criterion.

tolerance of the feedback mechanisms, which operate in final phases of the movement. In this case, there would be no decrease of the illusion effect in full-vision conditions, but large perturbations (as used by Castiello et al., 1993; Paulignan et al., 1991) would be corrected.

Second, the final phase of the grasp aperture might be controlled by continuously operating visual feed-forward mechanisms. These mechanisms would continuously monitor the size of the target object and adapt the grasp aperture accordingly. Such mechanisms would easily be able to correct the grasp aperture in a typical perturbation experiment, because here the grasp target changes visibly, and this change would be passed through the feed-forward mechanisms, leading to an adaptation of the grasp aperture. The feed-forward mechanisms would, however, not correct the grasp aperture in our illusion experiments, because here the grasp target never changes and therefore the feed-forward mechanisms would not change the movement plan.

Such feed-forward mechanisms might be faster than feedback mechanisms and might also have the advantage that they are still able to control the grasp aperture even if only the stimulus is visible but vision of the hand is occluded (because only the size of the grasp target is monitored). Such situations could easily arise in a natural environment. Also, ecologically it seems more likely that the grasp target changes visibly than that it is subjected to a visual illusion. Therefore, these advantages might outweigh the disadvantage of small errors in the artificial arrangement of a visual illusion. Note that we are only talking about the grasp aperture here. It could very well be that other aspects of the grasping movement are indeed under feedback control (e.g., the direction of the reach to the target).

The local minimum in the slopes that we found right before touching the grasp target (and that is "washed out" if we do not perform a touch-locked analysis) might be a further indication of such feed-forward mechanisms. Right before touch, the slope (or

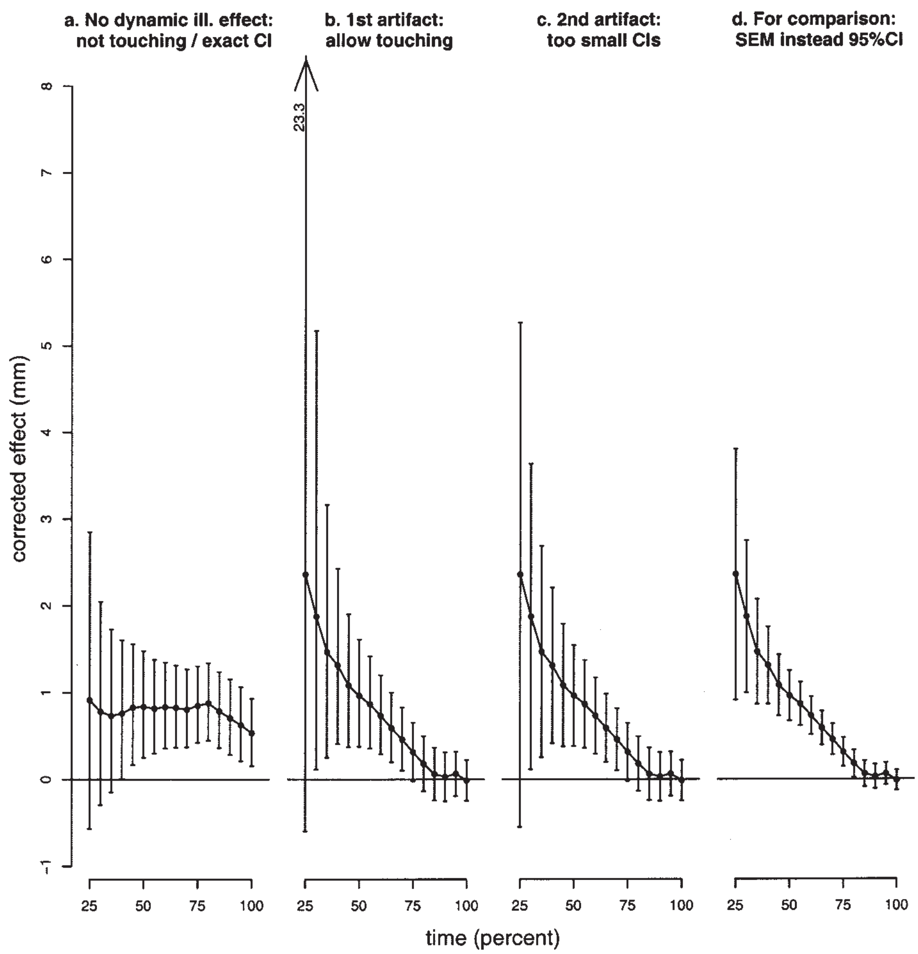

Figure 12. A summary of our results, which shows that two artifacts can lead to the impression of a dynamic illusion (ill.) effect. a: The corrected illusion effects, as found in Experiment 2 under full-vision conditions: There is no dynamic illusion effect. This plot corresponds to Figure 8c. Similar results were found in Experiment 1 under no-vision conditions. b. First artifact. We applied the Glover and Dixon (2002b) slow-velocity criterion to the same data as in Panel a. (This criterion was used in most studies by Glover & Dixon, 2002b; Glover et al., 2004). With this criterion, the time normalization includes time points at which the target object is already touched. This changes the whole normalized trajectories such that the corrected illusion effects seem to decrease to zero long before time (t) = 100% and also seem to be much larger at early time points. The vertical number (23.3) represents an upper confidence limit, which is beyond the scale of the figure. c: Second artifact. Here we used Glover and Dixon's (2002a, 2002b) statistical method to calculate confidence limits (CIs) for the data of Panel b. The error bars between $t = 25\%$ and $t = 35\%$ are much too small. d: Glover and Dixon (2002a, 2002b) typically showed *SEM* and not 95% confidence limits in their plots. For better comparison, we plotted the data of Panel c with the error bars depicting *SEM*. This plot looks like a clear replication of Glover and Dixon's dynamic illusion effect (e.g., see Figure 5 in Glover & Dixon, 2002a, or Figure 2 in Glover & Dixon, 2002b), but it is due to artifacts. Error bars in a, b, and c depict 95% confidence limits; error bars in d depict ± 1 standard error of the mean.

correlation) between physical size and grasp aperture decreases for a short time. This means that in the final phase of the movement the fingers are not "better" adjusted to the physical size of the grasp target (as we would expect from feedback mechanisms). Instead the fingers simply seem to close down until they touch the target object. This would be consistent with feed-forward mechanisms.

At this point, it seems difficult to decide between the two possibilities. We believe that further independent evidence is needed to clarify which of the two possibilities is more viable. But both possibilities can teach researchers something about the exact mechanisms that are used to control the grip aperture during final phases of reach-to-grasp movements.

Finally, we want to mention that our data have implications for theories that assume that grasping is not affected by visual illusions at all (Aglioti, DeSouza, & Goodale, 1995) or that the effects of visual illusions on grasping are due to obstacle-avoidance mechanisms and not the visual illusion per se (Haffenden et al., 2001). These theories propose that grasping should not be affected by the Ebbinghaus illusion if the distance between the central element and the context circles is the same for both variants of the illusion (i.e., for large and small context circles). We equated these distances in both experiments (at the cost of a reduced strength of the illusion). Also we used in Experiment 1 two versions of the illusion (far vs. near context), which enabled us to discriminate between obstacle-avoidance and perceptual sources of the illusion effects in grasping (this aspect of the experiment is discussed in depth in Franz et al., 2003). Nevertheless, we found similar effects of the illusion on perception and action in both experiments. This strengthens the idea that grasping is indeed affected by visual illusions in a similar way as perception (Franz, 2001; Franz et al., 2000; Pavani et al., 1999). A simple parsimonious explanation for all of these findings would be that the size of an object is calculated by a single process, which is affected by contextual visual illusions and serves perception as well as the motor system.

Conclusions

We tested Glover and Dixon's planning–control model of action (Glover, 2002, 2004; Glover & Dixon, 2001a, 2002a) with improved methodology. Contrary to the central assumption of this model, we did not find a dynamic decrease of the corrected effects of the Ebbinghaus illusion on grasping either under no-vision or under full-vision conditions. Instead, the illusion affected grasping from very early until very late phases of the reach-to-grasp movement (until right before touching the target object). We showed that the dynamic decrease found by Glover and Dixon (2002a, 2002b) was most likely artifactual. Taken together, our results question the central piece of evidence on which Glover and Dixon's (2001a, 2002a; Glover, 2002, 2004) planning–control model of action was built. Our results do not, however, question more classic notions of motor control (e.g., Woodworth, 1899) but might help researchers to learn more about the exact mechanisms that guide grasping movements.

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