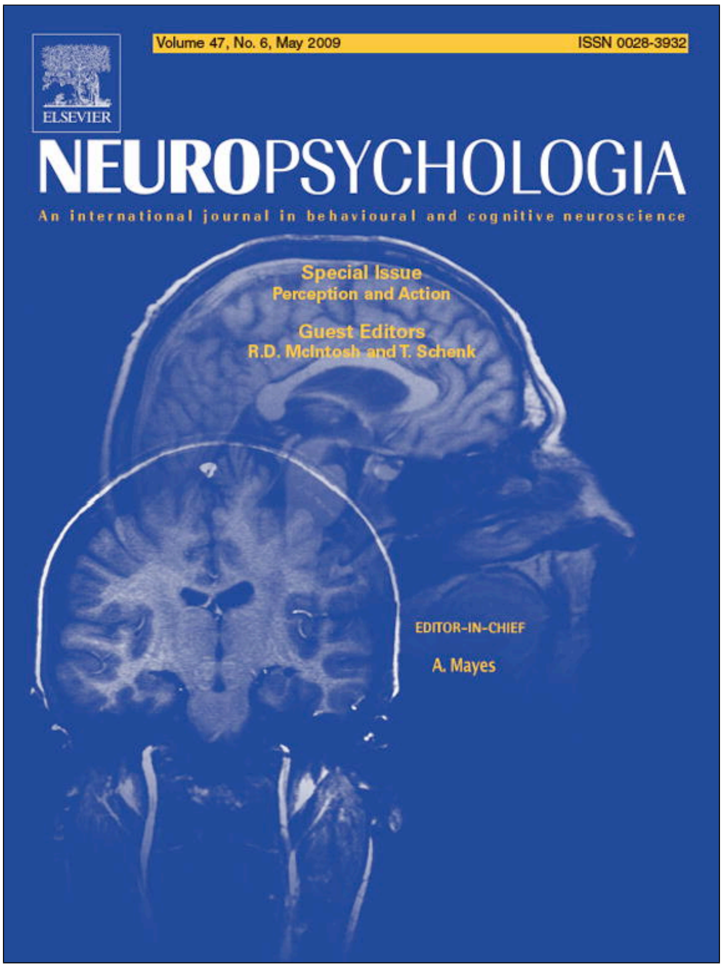
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Perseveration and contrast effects in grasping

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ABSTRACT

In order to assess sequential effects in grasping a disc, grip aperture was measured as a function of whether the previous disc was smaller or larger than the current target. In Experiment 1, a biphasic sequential effect was found over the course of the reach: Early in the movement, a contrast effect was observed in which grip aperture was wider following a smaller target; later in the movement, a perseveration effect was observed in which grip aperture was smaller following a smaller target. In Experiment 2, the target was accompanied by context discs that were larger and smaller than the range of target sizes. In this case, there was no contrast effect, and a perseveration effect was observed over the course of the movement trajectory. In a third experiment, a sequential contrast effect was found when subjects did not grasp the disc but merely estimated its size. Our interpretation is that there are two mechanisms producing sequential effects: a perceptual contrast effect in which the target appears larger following a smaller disc, and a motor perseveration effect in which subjects tend to reuse similar motor control parameters from trial to trial. These effects were overlaid in Experiment 1, producing the observed biphasic response. However, in Experiment 2, the context eliminated sequential perceptual contrast, and grip aperture only showed an effect of perseveration. In Experiment 3, only the perceptual effect was found because subjects did not need to grasp the disc.

An important theoretical issue in the study of motor control concerns effects of visual illusions. Often this issue has been investigated using illusions, such as the Ebbinghaus circles illusion, that are generated with simultaneous contrast between a target and the surrounding context (e.g., Aglioti, De Souza, & Goodale, 1995; Franz, Scharnowski, & Gegenfurtner, 2005; Glover & Dixon, 2002; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001). However, comparable perceptual effects might also occur due to sequential contrast. For example, a target may be judged as smaller if the target judged on the previous trial is larger or vice versa. In the present research, we investigated the effect of such sequential effects on grip aperture in a simple grasping task. The results suggest that there are two independent mechanisms that contribute to sequential effects: the first is a contrast effect that we believe is similar to the simultaneous contrast effect found with the Ebbinghaus illusion. The second is a perseveration effect in which the grasping trajectory tends to resemble that on the previous trial. The latter mechanism may be related to the repetition of motor programs on successive trials.

In our previous research, we have shown that simultaneous contrast effects are dynamic, so that they increase in magnitude as the hand begins to move and then decrease as the hand approaches the target (Glover & Dixon, 2001a,b, 2002). In our analysis, this is due to two competing trends: First, no contrast effect is expected at the onset of the reach because grip aperture initially is unrelated to the size of the target. Thus, effects of contrast must unfold gradually over time as the grip accommodates to the target. Second, visual and proprioceptive feedback serve to correct any invalid effects of context as the movement progresses, so that by the time the hand reaches the target, an accurate grasp can be accomplished. Together, these trends imply that effects of simultaneous contrast should at first increase over the course of the reach and then decrease.

Conceivably, the same type of effect might be produced with sequential contrast. The rationale is that it may be difficult to judge the absolute size of a target when it is presented in isolation against a uniform background, but it may be much easier at relatively short intertrial intervals to judge whether the target is larger or smaller than that presented on the previous trial. If subjects use such relative-size information, a target will tend to be seen as larger following a smaller target and smaller following a larger target. Such contrastive effects are sometimes found in perceptual judgment tasks (e.g., Schifferstein & Frijters, 1992). More generally, in multiple regression analyses of sequential effects, judgments of magnitude typically correlate negatively with the magnitude of the preceding stimulus (e.g., Jesteadt, Luce, & Green, 1977). Given that such effects are generally thought to be perceptual in origin, we anticipate that they would follow the same time course as effects of

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simultaneous contrast: they should increase over the initial course of the reach and then decrease as the hand approaches the target.

In addition to the potential for sequential contrast effects, there are reasons to expect perseveration effects in grasping. For example, Dixon (2002; see also Dixon & Glover, 2004; Dixon, McAnsh, & Glover, 2005) found that the manner of grasp on one trial tends to be similar to that on previous trials. For example, when subjects had to select between two plausible grasping postures, there was a strong tendency to reuse the posture from the previous trial. Similar perseveration effects were obtained by Rosenbaum and Jorgensen (1992) and Kelso, Buchanan, and Murata (1994). A general characterization of these results is that the grasp on one trial tends to resemble that on the previous trial. Although this effect has been investigated primarily with qualitatively different postures, there is some precedent for analogous effects with continuously varying motor parameters as well. For example, Jax and Rosenbaum (2007) found the amount of curvature in a pointing movement tended to be similar to that on the previous trial.

In sum, there are two possible sequential effects that might be observed in grasping: a size-contrast effect, in which the size of the preceding disc influences the perception of the size of the target disc on a given trial; and a perseveration effect, in which the response produced on a given trial tends to resemble that from the preceding trial. These two sequential effects differ in sign: following a smaller disc, size contrast implies that grip aperture should be larger but perseveration implies that grip aperture should be smaller. In the present research, we attempt to disentangle these two types of sequential effects on grasping.

1. Experiment 1

In the first experiment, we asked subjects to reach out and grasp a plastic disc in front of them. The stimuli varied in size from 26 to 34 mm in diameter in 2 mm steps, and the trials were arranged so that the immediately preceding trial used a disc that was either 2 mm larger or 2 mm smaller than the current stimulus. The empirical question was whether the size of the disc on the preceding trial would have an effect on grip aperture on the current trial.

1.1. Method

1.1.1. Subjects

Eight undergraduates at the University of Alberta served as subjects as part of a course requirement.

1.1.2. Apparatus

Subjects sat on an adjustable chair at a 100 cm × 120 cm table and viewed the table through liquid crystal goggles that could be either opaque or transparent (Milgram, 1987). On each trial, subjects reached and grasped a disc that was 26, 28, 30, 32, or 34 mm in diameter. The discs were made of 2.5 mm thick white plastic, and the edges were painted black. Before each trial, the disc was placed on a stand that raised it 10 mm off the surface of the table top. The stand was a truncated brass cone, 20 mm in diameter at the base and 10 mm at the top. A 10 mm diameter plastic "start" disc was fixed to the table, 10 cm from the edge of the table. Participants began each trial by placing their thumb and forefinger together on the start disc. The distance between the center of the start disc and the target was 28 cm.

Grip aperture during the reach was measured with an Ascension Technologies MiniBird electromagnetic motion-tracking system. Sensors were attached to the thumbnail, index finger nail, the wrist, and the elbow using medical adhesive tape. However, only data from the thumb and index finger were analyzed for the present purpose. Data were recorded from each sensor at 100 Hz with a resolution of 0.5 mm in three dimensions. The system had a RMS static positional accuracy of 1.8 mm averaged over the translational range of 180 cm. However, the effects of interest involved distance between sensors, and sampling of data from sensors a fixed distance apart indicated that distance measurements had a RMS accuracy of 0.51 mm. Moreover, data were averaged over successive samples, trials, and subjects. Based on such considerations, we estimated the standard deviation due to measurement error for contrast effects (such as those shown in Fig. 1) to be 0.03 mm, or about an order of magnitude smaller than the variability over subjects.

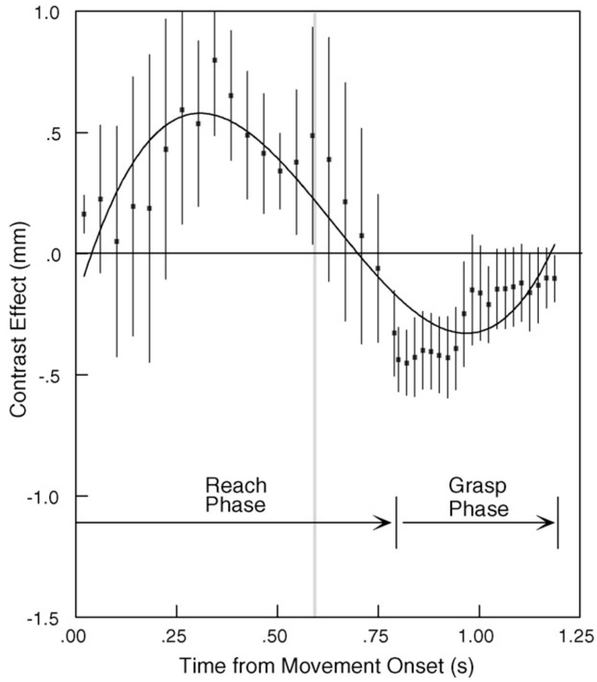

Fig. 1. Sequential contrast effect in Experiment 1, calculated as the difference between grip aperture following smaller discs and grip aperture following larger discs. Error bars represent the standard error over subjects, and the smooth curve is the fit of a cubic polynomial. The vertical gray line indicates the point of maximum grip aperture.

1.1.3. Procedure

On each trial, the liquid crystal goggles were opaque while the experimenter set up the disc for that trial. When the target stimulus was ready and the subject had his or her hand in the start position, the goggles were cleared to start the trial. The subject then reached and grasped the disc, lifting it momentarily off its stand. After the subject returned the disc to the stand, the goggles returned to an opaque state in preparation for the next trial. The median time between trials was 6.2 s, with an interquartile range of 5.4–7.2 s, and did not differ systematically between conditions. (The experimenter selected and set up the stimuli by hand on each trial, and as a consequence, the time between trials was not precisely controlled.)

1.1.4. Design

Subjects initially received a practice block of 10 trials in which each disc size was used twice in a random order. Following practice, subjects received 200 experimental trials. During these trials, the disc size was constrained to be either 2 mm larger or 2 mm smaller than that on the previous trial. Except for the largest and smallest sizes, moving to a larger or smaller size on the next trial was equally likely.

1.1.5. Analysis

An initial study of the data suggested that subjects typically moved relatively quickly to the vicinity of the target but then approached it slowly before reaching a minimum grip aperture as the disc was grasped. Consequently, we partitioned each reaching motion into two phases: the reach phase, starting from the point at which the thumb sensor attained a velocity of 0.05 m/s and ending when the velocity fell below 0.05 m/s in the vicinity of the target disc, and the grasp phase, from the end of the reach until the minimum grip aperture was attained. Both the reach and the grasp phases were divided into 20 equal-sized intervals, and the average grip aperture was estimated over each interval using linear interpolation. For each subject, these normalized grip-aperture measurements were averaged across trials for the 28, 30, and 32 mm discs, divided into trials preceded by a larger disc and those preceded by a smaller disc. (Data from trials using the 26 and 34 mm discs were not used since they were always preceded by a larger and a smaller disc respectively.) On 2.3% of the trials, there was no distinct grasp phase because the minimum grip aperture occurred simultaneously with the reach offset criterion; these trials were not used in the analysis. In addition, 0.2% of the trials could not be used because the movement onset or offset could not be identified using the velocity criterion.

In order to quantify the evidence for different interpretations of the results, linear models were fit to the results using linear mixed-effects analysis and the R program lmer (Bates & Sarkar, 2006; R Development Core Team, 2006). In mixed-effects analysis, estimates of both fixed and random effects are estimated directly from the data using maximum-likelihood techniques; the approach provides a more flexible and sometimes more powerful alternative to tools such as repeated-measures analysis

Table 1
Grip aperture (and standard error) in mm as a function of time, disc size, and preceding disc in Experiment 1[a].

Previous disc	Phase	Time (s)	Disc size (mm)		
			28	30	32
Larger	Reach	0.478	36.0 (1.8)	36.4 (1.8)	36.4 (1.8)
		0.640	54.1 (1.6)	55.2 (1.6)	56.7 (1.6)
		0.801	67.6 (2.7)	68.9 (2.7)	72.5 (2.7)
		0.963	73.3 (2.1)	75.9 (2.1)	78.1 (2.1)
		1.125	70.9 (0.9)	73.4 (0.9)	75.1 (0.9)
	Grasp	1.247	66.5 (0.7)	68.5 (0.7)	70.5 (0.7)
		1.331	64.2 (0.9)	66.0 (0.9)	67.7 (0.9)
		1.414	60.9 (1.1)	62.8 (1.1)	64.7 (1.1)
		1.497	57.3 (1.3)	59.3 (1.3)	61.2 (1.3)
		1.581	53.9 (1.3)	55.9 (1.3)	57.9 (1.3)
Smaller	Reach	0.478	36.6 (1.8)	35.9 (1.8)	36.7 (1.8)
		0.641	55.4 (1.6)	54.9 (1.6)	57.0 (1.6)
		0.804	68.2 (2.7)	69.8 (2.7)	72.8 (2.7)
		0.967	73.6 (2.1)	76.3 (2.1)	78.6 (2.1)
		1.130	70.7 (0.9)	73.1 (0.9)	75.4 (0.9)
	Grasp	1.253	66.0 (0.7)	68.0 (0.7)	70.2 (0.7)
		1.335	63.5 (0.9)	65.6 (0.9)	67.5 (0.9)
		1.416	60.6 (1.1)	62.7 (1.1)	64.5 (1.1)
		1.498	57.2 (1.3)	59.1 (1.3)	61.0 (1.3)
		1.580	53.7 (1.3)	55.7 (1.3)	57.8 (1.3)

[a] Although the data were normalized over 20 intervals in the reach and grasp phases, these numbers were averaged over five adjacent intervals for clarity of exposition here and in Table 2. The times reported are the midpoints of these composite intervals, measured from movement onset. Standard errors were derived from the standard errors of the parameter estimates of a linear mixed-effects model, excluding the variability due to the intercept.

of variance. Our approach to describing the evidence provided by the data was to fit pairs of models that differed by the inclusion of an effect of interest. (Such a strategy is used, for example, in hierarchical linear regression.) Models were compared by computing the maximum-likelihood ratio, that is, the likelihood of the data given the best fit of one model relative to that for the other model. Thus, if the likelihood ratio is very large (or very small), it would provide strong evidence in favor of one model relative to the other. However, the likelihood ratio by itself does not take into account the varying degrees of freedom in the two models, and the more complex model will always have a higher likelihood. Following the recommendation of Glover and Dixon (2004), this issue was addressed by adjusting the likelihood ratios for the differing number of parameters based on the Akaike Information Criterion (AIC; Akaike, 1973). Thus, this approach is tantamount to selecting the best model based on AIC values, a common technique in model selection procedures (e.g., Burnham & Anderson, 2002). In some prototypical hypothesis testing situations, an effect that is significant with $\alpha = 0.05$ would correspond to an adjusted likelihood ratio of about 3.

1.2. Results

The mean duration of the reach phase was 0.810 s (with a standard error of 0.054), and the mean duration of the grasp phase was 0.408 s (with a standard error of 0.057). Grip aperture over time is shown in Table 1 for each disc size, and the sequential contrast effect is shown in Fig. 1. The contrast effect was calculated at each point in time as the grip aperture on trials following a smaller disc less the grip aperture following a larger disc. As can be seen, during the middle portion of the reach, grip aperture was wider following a smaller disc than it was following a larger disc. (Note that in all three experiments, the measured grip aperture was larger than the actual grip aperture because the markers were attached to the outside of the finger and thumb. Thus, for example, measured grip aperture is larger than the size of the disc at the point of contact.) This conforms to the expectation based on a visual size illusion produced by the sequential contrast with the disc on the previous trial. However, this effect dissipated as the hand approached the target disc. Instead, during the final approach to the disc during the grasp phase, grip aperture was smaller following a smaller disc. In other words, a perseveration effect was obtained.

Evidence for this interpretation of the results was assessed by fitting nested linear models to the contrast data shown in Fig. 1. Effects over time were encoded as orthogonal polynomials up to degree 5, and these effects were assumed to vary randomly over subjects. A model that included a cubic trend provided the best fit. This fit was better than a null model with no time variation ($\lambda_{adj} = 6.26$), a model that incorporated only a linear trend ($\lambda_{adj} = 4.94$), and a model that included a quadratic trend ($\lambda_{adj} = 12.61$). Thus, the results provide clear support for the biphasic effect apparent in Fig. 1.

1.3. Discussion

Surprisingly, the results support both of the hypotheses concerning sequential effects. A size-contrast effect was observed early in the movement. This effect would seem to be comparable to the size-contrast effects observed by, for example, Franz et al. (2005). As found by Glover and Dixon (2002), the form of this effect was dynamic, in that it increased gradually over the beginning of the reach and then decreased as the hand approached the target. In addition, a perseveration effect was observed late in the movement. We hypothesize that this was produced by the same mechanism as the perseveration found when subjects select one of two possible postures (e.g., Dixon & Glover, 2004; Rosenbaum & Jorgensen, 1992). However, in this case, there was a range of possible grip apertures that might be used in any given case; the present perseveration effect suggests that the selected aperture tended to be similar to that selected on the previous trial.

Our interpretation of the biphasic sequential effect is that it represents a contrast effect and a perseveration effect overlaid on one another. First, the sequential contrast between different disc sizes on successive trials produces a visual illusion that the disc is larger (or smaller) than it actually is. In keeping with the model proposed by Glover and Dixon (2001a), the effect of such illusions should be apparent initially as the movement unfolds but is corrected online on the basis of visual and proprioceptive feedback. As with previous research with simultaneous contrast effects, this effect is gone before the hand contacts the target. At the same time, there is a smaller but longer-lasting tendency to repeat the grasp parameters used on the previous trial. This produces a perseveration effect (or negative contrast effect in Fig. 1). However, this is masked during the initial portion of the reach by the larger effect of the visual illusion and is only apparent during the final portion of the movement during the grasp phase.

Under some circumstances, a biphasic sequential effect can arise because of differences in timing. For example, if the time at which peak grip aperture occurred were simply delayed following larger discs, the difference between grip aperture following smaller discs and that following larger discs would be positive early in the reach (when peak grip aperture is attained following smaller discs but not yet attained following larger discs) and negative late in the reach (when the reverse is true). There are several reasons why such differences in timing cannot account for the current results. First, the inflection point in Fig. 1 is approximately at the end of the reach phase, so that sequential contrast is found in the reach phase and perseveration is found primarily in the grasp phase. However, during the normalization of the movement trajectories, the determination of the end of the reach phase was done independently for each movement. Thus, if peak grip aperture was delayed during the reach phase, it would have no effect on the pattern of results during the grasp phase. Second, there is no evidence in Table 1 that the time at which peak grip aperture occurs differs following larger or smaller discs. Rather, peak grip aperture tends to be smaller following larger discs and larger following smaller discs. Thus, it appears that the size of the preceding disc affects the magnitude of the grip aperture but not it's timing.

Our ability to identify the perseveration effect found at the end of the movement depends on our decomposition of the movement into distinct reach and grasp phases. It might not have been visible, for instance, if the movement were identified simply on the basis of a velocity criterion. In much previous work examining visual illusions and action, researchers have attempted to define the "end" of the movement so that it occurs prior to the object being physically contacted (e.g., Franz et al., 2005; Glover & Dixon, 2001a,b, 2002). The results of the present study imply that this practice is not always advantageous and that important insights into motor control can be found by examining the final approach and grasping phases of a movement (e.g., Lukos, Ansuini, & Santello, 2007).

2. Experiment 2

In Experiment 2, we evaluated our interpretation of the biphasic effect as consisting of two independent, overlaid trends. If this analysis is correct, one should be able to affect one mechanism but not the other. In particular, our prediction was that if the size-contrast effect were eliminated, one should observe a perseveration effect across the duration of the movement. The manipulation we used to eliminate the size-contrast effect was to provide a consistent context for the target on every trial. The context consisted of two discs, one just larger than the range of target stimuli and one just smaller. Our expectation was that the size of the target relative to the context would provide a strong cue to the veridical size of the disc that would minimize any illusory impression due to sequential contrast. This manipulation should not, however, have any impact on the perseveration effect. Indeed, based on past research (e.g., Dixon & Glover, 2004; Rosenbaum & Jorgensen, 1992) perseveration appears to result from a tendency of the motor system to use the outcomes of previous actions rather than the current perceptual information.

2.1. Method

2.1.1. Subjects

Twelve undergraduates served as subjects in exchange for course credit. Data from one subject were not used because of an anomalous movement trajectory in which he typically did not open his grip at all until well into the reach.

2.1.2. Apparatus, procedure, and design

The method was the same as in Experiment 1 except for the arrangement of the stimuli. The target disc was positioned on the stand as before, 20 cm from the start disc. A 24 mm context disc was placed 6 cm to the left of the target, and a 36 mm context disc was placed 6 cm to the right of the target. The median time between trials was 7.0 s, with an interquartile range of 6.2–8.4 s, and did not differ systematically between conditions.

2.1.3. Analysis

The analysis was the same as in Experiment 1. A small proportion of the trials (5.1%) were discarded because there was no distinct grasp phase; 0.4% further trials were not used because a reach onset or offset could not be identified based on the velocity criterion.

2.2. Results

The mean duration of the reach phase was 0.713 s (with a standard error of 0.029), and the mean duration of the grasp phase was 0.387 s (with a standard error of 0.038). Grip aperture for the reach and grasp phases of the movement are shown in Table 2, and the sequential effect is shown in Fig. 2. As can be seen, providing an uninformative context for the target disc eliminated any sequential contrast effect. Instead, a perseveration effect was found over most of the course of the movement trajectory. Although the effect evolved over the initial portion of the reach, the results differed from the dynamic pattern found in our previous studies (Glover & Dixon, 2001a,b, 2002) in that there was no clear evidence that the effect was eliminated by the time the hand approached the target. Indeed, the effect remained substantial at the end of the reach phase (which might have been defined as the end of the movement using previous methodology). The results are consistent with the interpretation that the perseveration effect remained until the grip closed and made physical contact with the target.

Table 2
Grip aperture (and standard error) in mm as a function of time, disc size, and preceding disc in Experiment 2.

Previous disc	Phase	Time (s)	Disc size (mm)		
			28	30	32
Larger	Reach	0.489	26.9 (1.0)	27.0 (1.0)	27.6 (1.0)
		0.632	54.9 (2.8)	56.0 (2.8)	58.6 (2.8)
		0.776	63.4 (1.9)	64.3 (1.9)	67.2 (1.9)
		0.919	65.0 (0.9)	67.2 (0.9)	69.2 (0.9)
		1.063	64.1 (1.2)	66.6 (1.2)	67.9 (1.2)
	Grasp	1.173	62.9 (1.5)	65.5 (1.5)	66.8 (1.5)
		1.249	60.2 (1.6)	62.4 (1.6)	64.3 (1.6)
		1.325	56.0 (1.6)	58.0 (1.6)	60.2 (1.6)
		1.401	51.6 (1.4)	53.6 (1.4)	56.0 (1.4)
		1.477	41.6 (2.7)	43.1 (2.7)	45.2 (2.7)
Smaller	Reach	0.483	27.2 (1.0)	26.5 (1.0)	27.1 (1.0)
		0.626	54.8 (2.8)	54.0 (2.8)	58.5 (2.8)
		0.770	62.5 (1.9)	63.4 (1.9)	66.8 (1.9)
		0.914	64.5 (0.9)	66.5 (0.9)	69.0 (0.9)
		1.058	63.4 (1.2)	65.9 (1.2)	67.8 (1.2)
	Grasp	1.167	62.5 (1.5)	64.7 (1.5)	66.5 (1.5)
		1.240	60.0 (1.6)	62.2 (1.6)	63.9 (1.6)
		1.314	56.0 (1.6)	58.0 (1.6)	60.0 (1.6)
		1.388	51.6 (1.4)	53.7 (1.4)	56.0 (1.4)
		1.462	42.0 (2.7)	40.5 (2.7)	43.8 (2.7)

Evidence for this interpretation was assessed by comparing the fits of nested linear models as before. A model that included a quadratic trend fit better than either a model that included no variation over time ($\lambda_{adj} = 3.62$), or a model that included only the linear trend ($\lambda_{adj} = 9.27$). There was little evidence that including the cubic trend improved the fit ($\lambda_{adj} = 1.30$).

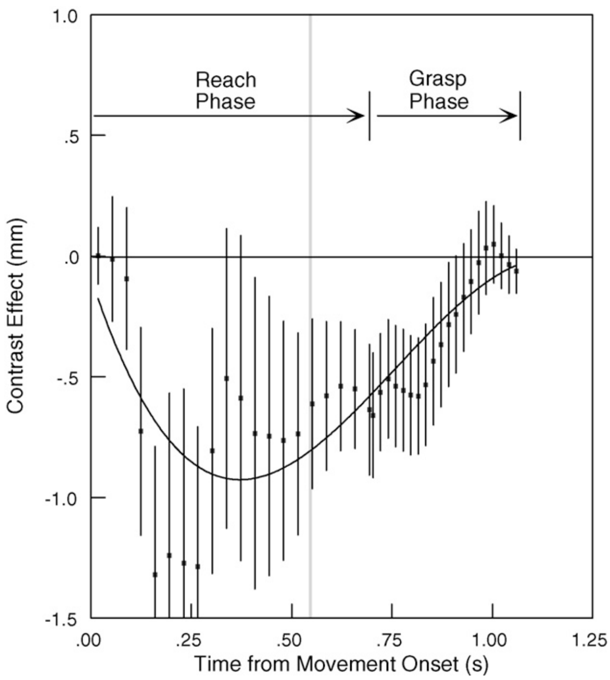

Fig. 2. Sequential contrast effect in Experiment 2, calculated as the difference between grip aperture following smaller discs and grip aperture following larger discs. Error bars represent the standard error over subjects, and the smooth curve is the fit of a cubic polynomial. The vertical gray line indicates the point of maximum grip aperture.

2.3. Discussion

The results demonstrate that incorporating the uninformative context discs eliminated the size-contrast effect observed in the early part of the reach in Experiment 1. Instead, a perseveration effect was observed over most of the reach trajectory. This pattern of results lends support to the interpretation of the previous biphasic pattern found in Experiment 1 as a short-lived contrast effect overlaid on a smaller but longer lasting perseveration effect. Our interpretation of the perseveration effect is that it is related to the role of memory in the control of action. Rosenbaum and Jorgensen (1992) suggested that aspects of a motor program might be held in working memory and reused if applicable to the current trial. Such an account would suffice for the present results if it is assumed that grip aperture is a feature that might be maintained in working memory in this way. Dixon, McAnsh, and Read (2008) suggested that important aspects of motor programs are retrieved from memory based on the current context and that the tendency to repeat the movement from the immediately preceding trial is essentially a memory recency effect. In either case, the present results imply that this effect is distinct from the sequential contrast effect and suggest that it involves a different mechanism than that involved in effects of visual illusions.

3. Experiment 3

In Experiment 3, we assessed whether the sequential contrast effect on perception that we hypothesized in Experiment 1 would be obtained if subjects did not grasp the disc but merely estimated its size. If the contrast effect we observed in that experiment was due to perceptual factors, the same result should be found for perceptual estimation under similar conditions.

3.1. Method

3.1.1. Subjects

Twelve undergraduates served as paid volunteers.

3.1.2. Apparatus and procedure

The apparatus and procedure on each trial was generally the same as in previous experiments. On each trial, a 26–32 mm disc was placed on the table at a distance of 20 cm from the start disc. However, when the goggles were cleared, instead of reaching and grasping the disc, subjects lifted their thumb and forefinger off the start disc and opened their grip to provide an estimate of the size of the disc. Generally, subjects increased their grip aperture as they lifted their hand away from the start disc, held their grip relative stable for several seconds, and then decreased their grip aperture as they returned their had to the start disc. The maximum grip aperture achieved during this motion provided a convenient index of grip aperture during this stable period and was taken as the dependent variable. The median time between trials was 6.7 s, with an interquartile range of 6.2–7.3 s, and did not differ systematically between conditions.

3.1.3. Design

As before, subjects completed 10 practice trials in which each of the discs appeared twice in a random order followed by 200 test trials. During the test trials, the preceding disc was either 2 mm larger or smaller than the current target, and the probability of moving to a larger or smaller disc (for the 28, 30, and 32 mm discs) was 0.5.

3.2. Results

The maximum grip aperture is shown as a function of current and preceding disc size in Table 3. On average, grip aperture was 1.2 mm larger for discs preceded by a smaller target than on those preceded by a larger target. The development of the contrast effect over time (up until the point of maximum grip aperture) is shown in Fig. 3.

To quantify the evidence for this effect, nested linear models were fit to the data. A model that incorporated an effect of preceding disc size fit better than that included only the linear effect of current target size ($\lambda_{adj} > 1000$). A model that included an interaction between current and previous disc size fit better still ($\lambda_{adj} = 645.35$), reflecting an increase in the magnitude of the contrast effect with disc size. We do not have a ready explanation for this interaction. However, one possibility is that it reflects a form of floor effect in which subjects tended to always open their grip at least a minimal amount during estimation, regardless of the size of the target. If that minimal aperture was close to the size of the smallest disc, it would tend to mask sequential contrast effects for that disc.

Table 3
Maximum grip aperture (and standard error) in mm as a function of current and preceding disc size in Experiment 3.

Preceding disc	Current disc size (mm)		
	28	30	32
Larger	46.0 (0.3)	48.0 (0.2)	50.0 (0.3)
Smaller	46.3 (0.3)	49.4 (0.2)	51.7 (0.3)

3.3. Discussion

The results provide converging evidence for our interpretation of the contrast effect observed in Experiment 1. We hypothesized that the effect on reaching was due to a sequential contrast effect on perception that caused the target to appear to be smaller or larger relative to the target on the previous trial. This was confirmed in the present experiment by asking subjects simply to estimate the size of the target disc. Consistent with this hypothesis, estimation demonstrated a contrast effect.

Interestingly, the contrast effect observed in the present estimation task was substantially larger than that observed in the reach phase of Experiment 1. However, our interpretation of the pattern of results in Experiment 1 is that the contrast effect early in the reach was overlaid with a smaller but longer-lasting perseveration effect that was only apparent in the grasp phase of the movement. On this

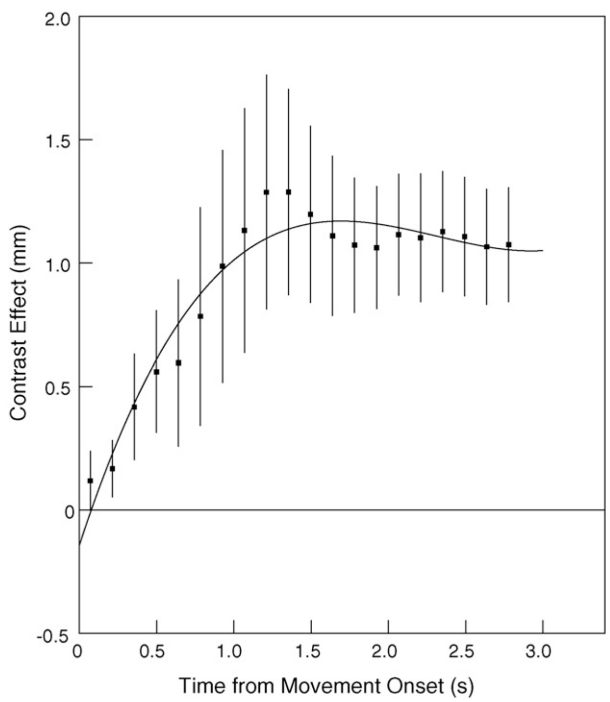

Fig. 3. Sequential contrast effect in Experiment 3 up until the point of maximum grip aperture, calculated as the difference between grip aperture following smaller discs and grip aperture following larger discs. Error bars represent the standard error over subjects, and the smooth curve is the fit of a cubic polynomial.

interpretation, the early contrast effect observed in Experiment 1 reflects the difference between two trends: a large positive contrast effect (perhaps commensurate with the results of Experiment 3) and a smaller perseveration effect. Thus, the larger contrast effect observed Experiment 3 is entirely consistent with our expectations.

Although a sequential contrast effect on perception is consistent with some evidence and theory in magnitude estimation tasks (e.g., Jesteadt et al., 1977), a more common finding is that subjects tend to repeat responses from previous trials (e.g., Lockhead & King, 1983). The present results would thus appear to be at variance with the usual result in magnitude estimation tasks. However, there are a number of differences between the present situation and that commonly used in magnitude estimation tasks. For example, the present experiment used a small number of stimuli whereas magnitude estimation tasks often use many more; estimation was done with a natural, continuous measure (grip aperture) rather than a verbal response; the stimulus was always just larger or smaller than that on the previous trial rather than being selected randomly; and subjects received no feedback on their estimates. Following Brown, Marley, Donkin, and Heathcote (2008), we ascribe the perseveration effects often observed in most magnitude estimation tasks to the process of translating internal representations of magnitude to one of a number of discrete responses, and such effects are likely to be minimal using the present response mode. In any event, the critical feature of the present design is that it replicates the configuration used in Experiment 1 and thus provides clear evidence that perceptual contrast effects contributed to the previous results.

4. General discussion

At a general level, the present results demonstrate the importance of memory in motor control. Indeed, both the size-contrast effect and the perseveration effect involve memory in some form. The size-contrast effect observed in Experiment 1 can be explained by assuming that perceptual estimates of the target's size depend in part on a comparison with the size of the target on previous trials. The perseveration effect entails perhaps a reuse or retrieval of aspects of the action performed previously. At a more specific level, the results of the three experiments together suggest the existence of two distinct mechanisms determining sequential effects, each of which can be manipulated independently. We hypothesize that the sequential size-contrast effect is comparable to simultaneous contrast effects that have been studied previously in investigations of the role of perceptual illusions in motor control (Aglioti et al., 1995; Franz et al., 2005; Glover & Dixon, 2001a,b, 2002), whereas the perseveration effect is related to the kinds of repetition effects observed by Dixon et al. (2008), Rosenbaum and Jorgensen (1992), and Kelso et al. (1994).

In the planning-control model proposed by Glover and Dixon (2001a, 2002) and Glover (2004), it is theorized that the initial planning of an action is affected by perceptual illusions such as those induced by simultaneous contrast. In reaching, for example, this implies that an effect of visual illusions is found early in the movement, as soon as the hand and trajectory begins to adapt to the target. However, the online control of an action is assumed to use different sources of information and consequently is less susceptible to such effects. Thus, the effect of the illusion is reduced as the movement unfolds and is often absent by the time the hand approaches the target. The size-contrast effect observed in Experiment 1 follows this general pattern, and we suspect that the same processes are responsible. In particular, movement planning may be affected by the size of the current target relative to the preceding disc, and the initial portions of the reach reflect this illusory effect. However, online-control mechanisms are relatively unaffected by sequential size-contrast effects just as they are relatively unaffected by context-induced illusions. As a consequence, whatever contrast effects exist on the planning of the grip, there is little remaining as the hand approaches the target.

In this context, the perseveration effect provides an interesting insight into the nature of online control. The effect was found throughout the movement trajectory and was substantial even at reach offset; the effect only disappeared at the point of minimum grip aperture as the hand physically closed on the target. This pattern suggests that unlike the size-contrast effect in Experiment 1, the perseveration effect is relatively unaffected by visual and proprioceptive feedback. In turn, this would imply that the control mechanism cannot be thought of as a simple feedback loop that modifies grip aperture to match the contours of the target. Indeed, such a conception would seem simplistic, since online control must be able to modulate actions in a wide range of circumstances with different grasps, targets, and functional goals. Thus, it is reasonable to suppose that an online-control mechanism must incorporate information about the grip posture that is appropriate in a given context, which in turn suggests that memory for previous grasps in that context would be relevant. Dixon and Glover (2004) framed this problem of controlling motor behavior as one of Bayesian estimation of motor parameters based on previous experience (see also Körding & Wolpert, 2004). From such a perspective, recent experience is more likely to be relevant than more distant experience and hence should have a greater effect on estimating the current movement parameter. The perseveration effect thus has the character of a memory recency effect.

The apparent independence of contrast and perseveration effects is likely due to independent neural origins. On the one hand, contrast judgments can plausibly be ascribed to the functioning of the human ventral visual stream in perception (e.g., Milner & Goodale, 1995). Conversely, perseveration effects may be related to the function of the frontal lobes. For example, perseveration in behavior is a core symptom of the so-called "frontal syndrome" that arises after damage to the frontal lobes, and Broca's aphasics show perseveration in speech patterns (Kolb & Whishaw, 2005). One possible explanation for perseveration is that performing a behavior primes that same behavior on ensuing trials, and in frontal patients the cortex that normally serves to inhibit the tendency to perseverate has been lost. Thus, although contrast and perseveration effects may both be evident in a given action, the former clearly has a motor origin whereas the latter has a perceptual origin.

The importance of memory processes in motor behavior that we and others have reported stands in contrast to many current views of motor control. In particular, Milner and Goodale (1995) in their "perception-action" model explicitly distinguished the role of memory in perception and action. In this view, perception is a relatively slow process in part because it relies heavily on the retrieval of memories of past experiences in order to make perceptual judgments and provide identifications, its main tasks. Conversely, the action system is argued to owe the relative speed of its processes to its ability to operate almost exclusively "online," making its spatiotemporal judgments in real time using *de novo* calculations. The fact that perseveration effects were found even at the end of the reach phase in the present study is one argument against such a characterization of the motor system. Rather, it would seem that the motor system also relies significantly on memory processes in formulating its plans, and, more interestingly, the online-control system appears to use memory as well in monitoring motor plans as they are carried out.

The present results also invite questions concerning the strength of perseveration effects and the extent to which they may generalize. In the present study, for example, the targets were nearly identical to discs presented previously, varying by only 2 mm from trial to trial. Moreover, the trials followed one another in relative quick succession. It seems likely that these conditions provided an optimal situation for observing perseveration effects. It may be interesting, therefore, to see if similar results occur with stimuli that differ more radically on successive trials.

Some answers to these questions may already exist. For example, Dixon et al. (2008), using a task in which subjects selected between two qualitatively different grasps, found that the tendency to repeat a grasp declined markedly if distinct objects were used on successive trials. Similarly, Dixon (2003) found that the tendency to repeat a pointing trajectory was reduced by changing the background context and the appearance of the target. Thus, we might anticipate that changing the form of the target object in the present paradigm would reduce the magnitude of the perseveration in grip aperture. On the other hand, the effect may be relatively long lasting: Both Dixon et al. (2008) and Jax and Rosenbaum (2007) found evidence that perseveration effects could last five or more trials. Presumably, the duration of the effect depends in the extent to which the intervening trials interfere with memory for the previous action, but this variable has not been investigated in detail.

In sum, the present results provide evidence for two sequential mechanisms in grasping. A size-contrast effect leads to an illusory percept that the target is larger or smaller based on its size relative to the previous target. In addition, a perseveration effect is a tendency to use the same grip aperture from the previous trial. The contrast effect is reduced over the course of reach and is largely absent by the time the hand approaches the target. However, the perseveration effect occurs throughout the movement and is eliminated only as the hand finally closes on the target.

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