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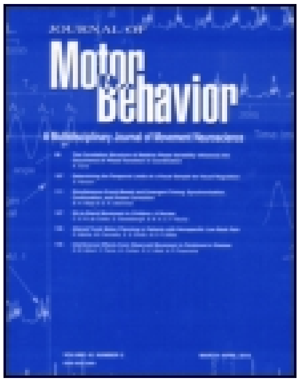

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Time Course Analysis of Closed- and Open-Loop Grasping of the Müller-Lyer Illusion

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Time Course Analysis of Closed- and Open-Loop Grasping of the Müller-Lyer Illusion

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ABSTRACT. The authors investigated whether the early or later stages of closed-loop (CL) and open-loop (OL) grasping movements were differentially influenced by the Müller-Lyer (ML) illusion. Participants ($N = 21$) reached out and grasped small (5 cm) and large (7 cm) objects embedded within fins-in and fins-out ML configurations. Grasping time (GT) was normalized, and absolute grip aperture (GA) as well as scaled illusion effects were computed at 20%, 40%, 60%, and 80% of GT. The results indicated that CL trials were refractory to the illusory array (i.e., from 20% to 80% of GT), whereas OL trials were influenced by the ML figure during that same time. Those findings suggest that CL trials were supported by unitary and metrical visual information, whereas OL trials were entirely supported by perception-based visual information.

Key words: closed-loop, dynamic illusion effect, grasping, Müller-Lyer illusion, open-loop

An emerging issue in the visuomotor control literature relates to the time course in which the visuomotor system attenuates the perceptual size illusions induced by pictorial arrays such as the Müller-Lyer (ML) figure. On the one hand, there is evidence to suggest that visually guided reaching and grasping movements are entirely refractory to the illusion-inducing elements of pictorial displays (e.g., Danckert, Sharif, Haffenden, Schiff, & Goodale, 2002)—a finding consistent with Goodale and Milner's (1992) influential perception/action model (PAM; see Milner & Goodale, 1995, for an extensive review). According to the PAM, visually based movements are refractory to the context-dependent properties of illusory arrays because dedicated visuomotor networks residing in the dorsal visual stream support such actions. Those dorsal stream networks are thought to compute absolute (i.e., Euclidean) object features and metrically precise movement parameters at the time of response planning, whether or not the hand and target are visible during the response (Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000; Westwood & Goodale, 2003).

On the other hand, Glover and Dixon (2002) have recently proposed that pictorial illusions elicit a dynamic effect on motor output. For instance, they observed that the Titchener circles illusion influenced the early but not the later stages of grip formation. On the basis of those and other data, Glover (2004; see also Glover & Dixon, 2001a, 2001b) proposed a model that incorporates separate visual representations for the planning and control of action (the planning/control model [PCM]; see Woodworth, 1899, for historical context). According to the PCM, a context-dependent planning representation supports the initial kinematic parameterization of the action, whereas a context-independent control representation gradually asserts influence as the action unfolds. Interestingly, the PCM states that in the absence of visual feedback during the response, the control representation accesses nonvisual sources of information (e.g., efference copy and proprioceptive or memory-based information, or both) to resolve the initially biased motor plan—with the caveat that visual feedback provides a more complete attenuation of the illusion.

The contention that visual illusions influence the early but not the later stages of grasping represents a notable contribution to the visuomotor control literature because it suggests that single measures of grip formation (e.g., peak grip aperture) may obscure illusion effects that occur either before or after the chosen measure. The PCM is tempered, however, by the results of two recent studies that failed to identify dynamic illusion effects in grasping. In both studies, an open-loop (i.e., target and hand occlud-

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ed at movement onset) grasping response was directed to a target disk embedded in the Titchener circles illusion. In the first study, Danckert et al. (2002) reported that absolute grip aperture (GA) was refractory to the illusory effects of the pictorial display from 25% to 100% of the time to peak grip aperture. In the second study, Franz (2003) found that the illusion did intrude into the motor response and that the effect of the illusion remained "remarkably constant" over time (p. 211). According to Franz, the between-experiments discrepancy related to the fact that Danckert et al. did not use corrected (i.e., scaled) illusions effects to account for the fact that visual object features do not have a constant effect on GA throughout the grasping response (see also Glover & Dixon, 2002).

Our goal in this investigation was twofold. First, we sought to determine the time course in which closed-loop (CL) and open-loop (OL) grasping movements may resolve the context-dependent properties of the ML illusion. To our knowledge, this study represents the first systematic attempt to compare the dynamic effects of that illusion in either CL or OL visual conditions. Second, we measured absolute grip aperture (GA) and scaled illusion effects to bridge the gap between existing studies of dynamic illusion effects. We examined dynamic changes in GA by normalizing grasping time (GT) and computing GA at 20%, 40%, 60%, and 80% of GT. If the PAM is correct, then the context-dependent properties of the ML figure should not influence the unfolding trajectory of CL or OL trials. Recall that within the PAM, the dorsal visual pathway computes metrical movement parameters in real time (i.e., at the time of response cuing), thus accounting for the equivalent predictions for CL and OL trials (Haffenden & Goodale, 1998; Westwood & Goodale, 2003). If, however, the PCM is correct, then the ML illusion should have a reliable impact on GA during the early stages of the action, with gradual attenuation of the illusion as the action unfolds in time. Moreover, that time-dependent resolution of the perceptual illusion should be more pronounced in the CL than in OL trials.

Materials and Method

Participants

Twenty-one right-handed individuals (11 men, 10 women) ranging in age from 19 to 26 years participated in this study. All had normal or corrected-to-normal vision and were naive as to our exact purpose in the experiment. This research was performed in accordance with guidelines established by the Office of Human Research, Indiana University.

Apparatus

Stimuli consisted of 5- and 7-cm fins-in and fins-out ML configurations (30° fin angles) printed in black ink on white cards (15 cm × 9 cm). We created a graspable object by placing an appropriately sized black wooden bar over the shaft of the ML figure (5 cm or 7 cm length × 0.7 cm height × 0.7 cm width). The participants' midline was oriented perpendicularly to the long axis of the ML figure. For each trial, a single-target array was presented on a blackened table surface at a distance of 35 cm from a home position located at the participants' midline; hence, grasping the object required 35 cm of limb displacement in the depth plane. We controlled vision of the aiming environment via liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, ON, Canada), an interval-timing device, and a telegraph key (i.e., the home position) located 5 cm from the edge of the table. The stimuli used in this investigation have been shown to reliably bias perceptual judgments (i.e., a manual estimation task) of object size (e.g., Heath & Rival, 2005; Heath, Rival, & Binsted, 2004; Westwood, Chapman, & Roy, 2000; Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2002).

Procedure

Participants stood for the duration of the experiment, and we instructed them to reach toward and grasp the target object "as naturally as possible" from within the target array in two visual conditions (see the following). Participants used their right hand and initiated their grasping movement with their thumb and index finger pinched lightly together. Each trial began with a 2-s preview phase in which the shutter goggles were set in their transparent state, thus providing vision of the target array and grasping environment. In the CL visual condition, following the preview phase, an auditory tone signaled participants to begin their reaching movements; the goggles remained in their transparent state for the duration of the trial. In the OL condition, the auditory tone signaled participants to initiate their reaching movement following preview, and the goggles reverted to their opaque state coincident with participants' release of pressure from the home position; hence, vision of the environment was available during the planning but not the control stage of the grasping movement.

Participants performed 10 trials for each of the four target arrays in each visual condition for a total of 80 trials. Visual conditions were blocked and counterbalanced, with the order of target arrays within visual conditions presented in a pseudo-randomized fashion.

Data Collection and Reduction

We placed infrared-emitting diodes (IREDs) on the lateral edge of the index finger, the medial edge of the thumb, and the styloid process of the wrist. We collected three-dimensional positional data by using an OPTOTRAK 3020 system (Northern Digital, Waterloo, ON, Canada) sampling at 200 Hz for 2 s. We filtered position data offline by using a second-order, dual-pass Butterworth filter with a low-pass cut-off frequency of 15 Hz. Subsequently, we calculated instantaneous velocities by differentiating the displacement data, using a three-point central finite difference algorithm. Movement onset was defined as the first sample frame after which resultant thumb velocity attained and maintained a value of 50 mm/s for 10 consecutive frames (50 ms). Movement offset was defined via a two-step procedure. First, thumb velocity had to fall below a criterion of 50 mm/s. Second, we marked for movement offset the first sample frame from within the velocity criterion in which no further thumb displacement was detected anterior to the body (i.e., primary movement direction). We used a two-step procedure so that any response initially overshooting the target object was not incorrectly marked (e.g., Elliott, Heath, et al., 1999).

The time between movement onset and movement offset was defined as GT. We normalized GT and measured GA (absolute distance between thumb and index finger) at 20%, 40%, 60%, and 80% of GT. In addition to reporting absolute GA, we computed scaled illusion effects because it has been argued that one must scale GA to obtain an unbiased measure of the impact of the illusion at different points in the grasping trajectory (e.g., Franz, 2003; Glover & Dixon, 2002). We determined scaled illusion effects by calculating the ratio of the mean illusion effect (i.e., mean GA for the fins-out ML figure minus mean GA for fins-in ML figure) divided by the slope of the GA to object-size function for each participant and time point (Franz; see also Franz, Fahle, Bulthoff, & Gegenfurtner, 2001). Most important, scaled illusion effects in combination with absolute GA data provided the means to determine if the ML illusion elicited a time-varying impact on grasping.

Results

We interpreted all omnibus tests by using an alpha level of .05. Where appropriate, we corrected *F* statistics for violations of the sphericity assumption by using the appropriate Huynh–Feldt correction. We explored significant effects and interactions arising from those analyses via simple effects analyses and a Bonferroni correction for multiple comparisons ($p < .05$).

We examined absolute GA via 4 (time: 20%, 40%, 60%, 80% of GT) × 2 (vision: CL, OL) × 2 (size: small, large) × 2 (illusion: fins-in, fins-out) fully repeated-measures analyses of variance (ANOVA). The results for GA revealed significant main effects for time, $F(1.6, 33.8) = 196.14$, $p < .001$, vision, $F(1, 20) = 13.75$, $p < .01$, size, $F(1, 20) = 296.88$, $p < .001$, and illusion, $F(1, 20) = 23.93$, $p < .001$, as well as interactions involving Time × Vision, $F(1.9, 41.9) = 13.27$, $p < .001$, Time × Size, $F(2.4, 48.7) = 70.45$, $p < .001$, and Vision × Illusion, $F(1, 20) = 8.72$, $p < .001$. We preface the description of each interaction with a general description of the effect of time. Specifically, as can be seen in Figure 1, GA accumulated from 20% to 60% of GT and then plateaued (significant second-order polynomial), $F(1, 20) = 28.71$, $p < .001$ (see Jeannerod, 1984, for a complementary finding). The Time × Vision interaction indicated that CL and OL trials did not differ at 20% or 40% of GT, *t*s(20) = 1.80 and 1.71, respectively, *p*s > .05; however, at 60% and 80% of GT, GA was greater for OL trials than for CL trials, *t*s(20) = 5.43 and 5.83, respectively, *p*s < .001. Analysis of simple effects for the Time × Size interaction did not indicate that the different targets elicited a time-varying impact on GA; rather, GA was always smaller for the 5-cm target than for the 7-cm target: At 20%, 40%, 60%, and 80%, respectively, *t*s(20) = 4.98, 10.47, 19.02, and 24.36, *p*s < .001. Last, the Vision × Illusion interaction showed that GA was reliably greater for the fins-out ML figure than for the fins-in ML figure for OL trials, $t(20) = 6.30$, $p < .001$, but not for CL trials, $t(20) = 0.99$, $p > .05$ (see Figure 1).

Scaled illusion effects were subjected to 4 (time: 20%, 40%, 60%, 80% of GT) × 2 (vision: CL, OL) fully repeated-measures ANOVA. The results elicited a significant effect of vision, $F(1, 20) = 4.45$, $p < .05$: Scaled illusion effects were greater for OL than for CL trials (see Figure 2 and Table 1).

Mean GTs were equivalent for CL (918 ms) and OL (908 ms) trials, as were mean GTs for small (910 ms) and large (916) target objects. Last, GT for the fins-in (919 ms) and fins-out (907 ms) ML figures did not differ.

Discussion

In this investigation, we sought to determine the time course in which CL and OL grasping movements resolve the perceptual effects of the ML figure. We measured absolute GA and scaled illusion effects to compare our results with those of all extant studies on that topic. We reasoned that CL and OL actions should be insensitive to the ML illusion at all temporal points if the PAM is correct. In contrast, according to the PCM, CL and OL actions should show early evidence of illusion effects, with those effects decreasing over time for both types of actions, but to a greater extent for the CL trials.

Effect of the ML Figure in CL Grasping

The CL grasping movements studied here were refractory to the ML illusion. As indicated in Figure 1, absolute GA did not reveal an illusory bias matching the well-documented perceptual effects of the ML illusion (e.g., Heath & Rival, 2005; Heath, Rival, et al., 2004; Westwood, Chapman, et al., 2000; Westwood, Heath, et al., 2000; Westwood et al., 2002). In other words, the fins-in and fins-out ML configurations were not reliably different at any point in time studied here (i.e., 20% through 80% of GT). In line with that finding, in our analysis of scaled illusion effects we found no evidence that the ML figures elicited a time-varying effect on motor output. Thus, the absolute GA data in combination with the scaled illusion effects indicated that CL trials were immune to the illusion-evoking properties of the ML figure during the early and later stages of grasping—a finding congruent with a number of reports that static and absolute measures of CL grasping control (e.g., peak grip aperture) are mostly, if not entirely, resistant to pictorial illusions (e.g., Aglioti, DeSouza, & Goodale, 1995; Brenner & Smeets, 1996; Hu et al., 1999; Jackson & Shaw, 2000; Westwood, Chapman, et al.; Westwood, Heath, et al.; Westwood et al.; but see Daprati & Gentilucci, 1997).

The notion that CL trials do not fall prey to the ML illusion is compatible with the PAM (Goodale & Milner, 1992). Within the PAM, that finding is accounted for by the fact that CL grasping is mediated by metrically precise dor-

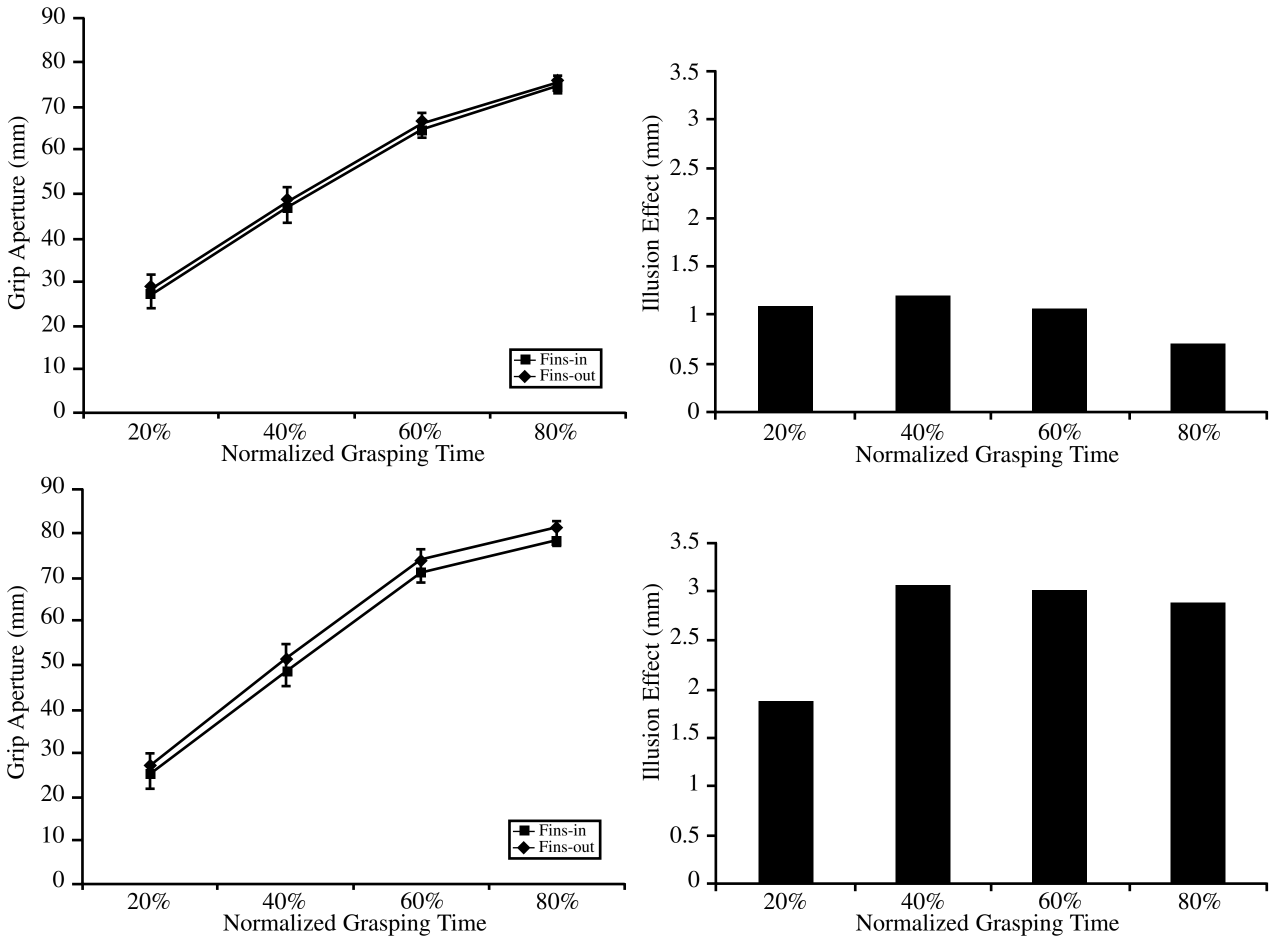

FIGURE 1. The effect of the fins-in and fins-out Müller-Lyer configurations on grip aperture (mm) in closed- (**top panel**) and open-loop (**bottom panel**) visual conditions as a function of 20%, 40%, 60%, and 80% of grasping time. Offset bar graphs depict mean illusion effect (fins-out minus fins-in) at each time point. Error bars (line graphs only) represent standard error of the mean.

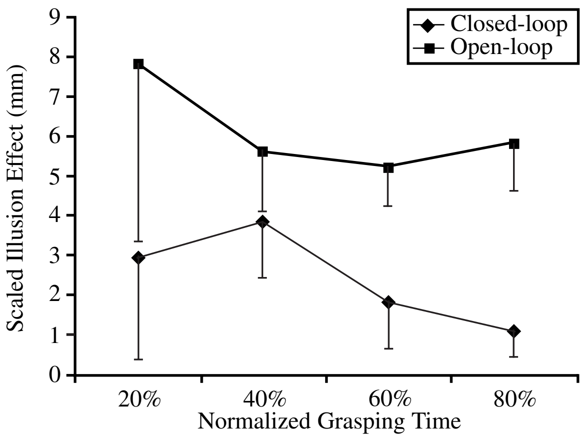

FIGURE 2. The scaled illusion effects (mm) on grip aperture at 20%, 40%, 60%, and 80% of grasping time for closed- and open-loop visual conditions. Error bars represent standard error of the mean.

sal stream mechanisms that operate without the influence of the contextual information driving perception. Moreover, because dorsal stream mechanisms operate in real time, they are thought to be engaged at the time of response cuing and throughout the response (Westwood & Goodale, 2003). Thus, the PAM provides a tenable model for explaining the absence of illusory effects during the early and later stages of CL grasping. Most interesting, however, only Glover and Dixon (2002) measured the impact of a visual illusion (the Titchener circles) over the time course of CL grasping. In Experiment 1 of that work, Glover and Dixon found that the Titchener circles illusion intruded into the early but not the later stages of a motor response.[1] That dynamic illusion effect was taken as empirical support for the PCM's contention that independent representations underlie grasping control: a context-dependent planning representation that supports initial kinematic parameterization of the action and a later-occurring and context-independent control representation that supports the later stages of action.

TABLE 1. Mean (*M*) and Between-Participants Standard Error of the Mean (*SEM*) for Illusion Effect, Slope, and Scaled Illusion Effect as a Function of Normalized Grasping Time and Visual Condition

	Illusion effect[a]		Slope[b]		Scaled illusion effect[c]	
Visual condition	*M*	*SEM*	*M*	*SEM*	*M*	*SEM*
20% normalized grasping time						
Closed-loop	1.08	0.64	0.15	0.04	2.95	2.58
Open-loop	1.86	0.77	0.18	0.02	7.52	4.50
40% normalized grasping time						
Closed-loop	1.21	0.69	0.43	0.06	3.82	1.50
Open-loop	3.05	0.70	0.56	0.05	5.60	1.49
60% normalized grasping time						
Closed-loop	1.07	0.74	0.66	0.04	1.74	1.10
Open-loop	3.01	0.60	0.62	0.04	5.20	0.95
80% normalized grasping time						
Closed-loop	0.70	0.44	0.69	0.02	1.04	0.61
Open-loop	2.89	0.51	0.55	0.03	5.80	1.18

Note. Scaled illusion effects were calculated individually for each participant via the participant's own illusion effect and slope (see Franz, 2003, for complete details). Hence, it is important for the reader to bear in mind that one cannot directly compute scaled illusion effects on the basis of the illusion effect and slope values shown in the table because those values represent averaged means across participants. [a]Fins-out minus fins-in, in mm. [b]Grasp aperture (GA) to object-size function, in mm. [c]Illusion effect divided by slope.

The discrepancy between the present results and those of Glover and Dixon (2002) may relate to the type of stimulus array used in the latter investigation. Specifically, Glover and Dixon used the traditional small and large Titchener circles illusion in which target–flanker separation was less in the small-circles array than in the large-circles array. As indicated by Haffenden et al. (2001), surrounding annuli in the traditional small-circles array may be treated as obstacles, thereby influencing the control of visually derived actions. Indeed, when target–flanker separation is held constant, the Titchener circles illusion has been found to not influence motor output (Haffenden et al.; see also Danckert et al., 2002). Although Haffenden et al. examined OL trials, it has been shown in other reaching paradigms that two-dimensional objects within a reaching path can elicit an even more salient impact on CL actions (Krigolson & Heath, 2004; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999). Consequently, it is possible that the dynamic illusion effect reported by Glover and Dixon does not represent online attenuation of the context-dependent properties of the Titchener circles illusion; rather, GA modification or modifications during the later stages of the trajectory may reflect increased reliance on feedback-based resources so that contact with surrounding flankers in the small-circles array can be avoided.

In accord with the PAM (Goodale & Milner, 1992), we propose that CL grasping of an object embedded within a ML illusion is mediated by unitary and metrical visuomotor mechanisms residing in the dorsal visual pathway.

Effect of the ML Figure in OL Grasping

In the OL condition, vision of the hand and target object was occluded at movement onset. With that manipulation, absolute GA for the fins-out ML figure was greater than that associated with the fins-in ML figure at each time point studied here (i.e., 20% to 80% of GT). In terms of the scaled illusions effects, that metric did not yield a time-varying impact on motor output; however, OL trials produced larger scaled illusion effects than did their CL counterparts. In conjunction, absolute GA data and scaled illusion effects demonstrated that the absence of continuous visual input from the grasping environment resulted in a reliable illusory bias that was not resolved for upward of 80% of GT.

The findings just described are consistent with neither the PAM nor the PCM. According to the PAM, the illusion should not influence GA at any point during the OL action because the real-time visuomotor networks in the dorsal stream would have been engaged for movement programming at the time of response cuing (e.g., Haffenden &

Goodale, 1998; Haffenden et al., 2001; Hu et al., 1999; Hu & Goodale, 2000; Westwood & Goodale, 2003). In contrast, according to the PCM, the initial sensitivity of the OL action to the illusion should have decreased as the action unfolded. We base that view on the PCM's assumption of a transfer from a context-sensitive to a context-insensitive representation regardless of the availability of online visual feedback (Glover, 2004).

Why then were OL grasps susceptible to the ML figure throughout the grasping response? One possibility raised by Franz (2003; see also Franz et al., 2001) is that the visual-processing mechanisms associated with perceptual judgments and visually derived actions are one and the same. In support of that view, Franz found that the scaled illusion effects associated with the traditional small and large Titchener circles illusion influenced OL grasping from 25% to 100% of the time to peak grip aperture. Although Franz's formulation supports the OL movements studied here, it does not explain the refractory nature of our CL trials. Certainly, if a common internal representation was used for perception and grasping, then OL and CL grasping should be similarly influenced by the ML figure.

An alternative possibility is that online visual feedback is important in determining visuomotor resistance to the ML figure. Although that idea is tempered by some reports of the immunity of OL grasping to visual illusions (e.g., Danckert et al., 2002; see also Haffenden & Goodale, 1998; but see Mon-Williams & Bull, 2000), advance knowledge that visual feedback will be withdrawn during a movement can encourage participants to plan the spatiotemporal characteristics of their grasping trajectory before response cuing. In other words, OL grasping can produce a control strategy wherein the trajectory of an upcoming response is formulated offline (Glover, 2004) via a perception-based (Goodale & Milner, 1992) representation of the grasping environment. Two lines of evidence support our hypothesis. First, Heath and colleagues (Heath & Rival, 2005; Heath, Rival, et al., 2004; see also Westwood, Heath, et al., 2000) have shown that formulating GA to the perceived size of an object embedded within the ML figure in advance of grasping elicits a reliable illusory bias that is not attenuated for upward of 80% of grasping time. They attributed that finding to an explicit control strategy wherein participants specify their GA parameters offline (i.e., before response cuing) via an obligatory visual representation that is susceptible to pictorial illusions. Second, when participants are made aware that continuous visual input from the grasping environment (i.e., vision of the limb and target) will not be available during an upcoming movement, they tend to formulate their movement parameters in advance of response cuing and execute their response without online trajectory modifications (i.e., via central planning mechanisms; see, e.g., Binsted & Heath, in press; Elliott, Binsted, & Heath, 1999; Elliott, Heath, et al., 1999; Heath & Westwood, 2003; Heath, Westwood, & Binsted, 2004; Jakobson & Goodale, 1991). Therefore, we propose that the reliable illusory bias associated with our OL trials is related to a specific visuomotor strategy in which the spatiotemporal characteristics of an upcoming response are specified offline via perception-based visual information.

In sum, the OL grasping movements studied here demonstrated that real-time visual input from the grasping environment was not sufficient to implement a refractory grasping movement. In addition, the early bias of the illusion was not resolved over the course of the grasping response. That finding is consistent with neither the PCM nor the PAM. Instead, the reliable illusory effect observed here suggests that the early and later stages of OL grasping were specified offline via a unitary and perception-based visual representation.

Conclusions

CL trials were refractory to the ML illusion at each time point studied here (i.e., 20% to 80% of GT), whereas OL trials were influenced by the illusion during the same time period. Those findings are inconsistent with Glover's (2004; see also Glover & Dixon, 2002) PCM and with the elicitation of dynamic illusion effects. In terms of the PAM, the refractory nature of CL trials combined with the absence of a time-varying effect on motor output support the notion that unitary and real-time visual-processing mechanisms mediate online grasping control. It is, however, important to note that the constant illusion effects found in our OL trials contradict the assertion in the PAM that metrical movement parameters are specified at the time of response cuing. Instead, we propose that OL trials were tricked by the ML figures because participants evoked a mode of grasping control in which grasping parameters were specified offline via a perception-based representation of the visual environment.

NOTE

1. Most interesting, Experiment 2 of Glover and Dixon (2002) did not yield statistical support for a dynamic illusion effect. Although vision trials in that work elicited a reliable illusion effect, the effect remained constant over time.

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