#### Opinion

support this theory contains unintended classical grouping cues that are themselves likely to be responsible for any grouping percepts. These grouping cues are consistent with well-established grouping mechanisms and processes. Furthermore,

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when these cues are removed while preserving the temporal synchrony cue, the resulting stimuli no longer promote grouping. There is, therefore, no reason to posit the existence of novel synchronysensitive mechanisms or processes.

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# Visual illusions affect planning but not control

## Scott Glover

Much debate has arisen over how to account for the pattern of effects of visual illusions on action – that is, the findings that illusions affect actions in some circumstances but not others. I propose that this pattern can best be explained by postulating that visual illusions affect the planning of actions but do not affect the on-line control of actions. Strong evidence for this viewpoint comes from recent studies that show 'dynamic illusion effects': a large illusion effect early in a movement, but a decreasing effect as the hand approaches the target. These findings pose difficulties for other models of illusion effects on action.

Scott Glover Dept of Psychology, Pennsylvania State University, 541 Moore Bldg, University Park, PA 16402, USA. e-mail: srg13@psu.edu Much recent work in the visuomotor domain has been aimed at uncovering, cataloguing and explaining the effects, and non-effects, of visual illusions on actions. Many studies have suggested that visual illusions do not affect actions as much as perceptions [1–8], whereas others have suggested that such dissociations depend on different factors [9–12], or do not exist at all [13–15]. Some recent studies have indicated that the effects of illusions on action might be larger in the early stages of a movement than later during the movement [16–21]. Here I offer a critique of three models recently put forward in this journal [22–24], and I describe some of the evidence for and against each. I propose an alternative explanation of the effects of illusions – the 'planning–control' model – which can also account for the dynamic illusion effects found in several studies of illusions and action [16–19].

Current models of illusion effects on action A currently popular model of illusion effects on action is the 'perception-action' model [25,26]. This model posits that the ventral and dorsal visual pathways in the brain provide the visual bases of perception and action, respectively. The perception-action model has gained support from examination of patient 'DF', who has damage to the ventral cortical pathway. DF exhibited severely impaired perceptual abilities coupled with relatively intact visuomotor performance [27,28].

Behavioral support for the perception–action model has come from studies in which visual illusions were shown to have smaller effects on actions than on perceptions. In an early study, Aglioti *et al.* showed



**Fig. 1.** Some of the illusions used in studies of illusions and action. (a) The Titchener size-contrast illusion (see [1,2,5,8,13,15,19]). In experiments assessing action, the center circles are replaced with discs that the participants must grasp. In some studies the grasp was less affected by the illusion than a perceptual judgment [1,2,5,8]. In other studies the effects were similar [9,10], or decreased over time [15]. (b) The horizontal-vertical illusion (top), and as it appeared in Vishton *et al.* [9] (bottom). Participants had to pantomime a grasp of the triangle with the thumb on the bottom, and the index and middle fingers on the top. Vishton *et al.* found that the distance between the index and middle fingers. (c) The tilt illusion used by Glover and Dixon [16–18]. A bar was grasped from a background grating. Effects of the illusion on hand orientation were large early in the reaches, but decreased continuously as the hand approached the bar. (d) The Muller-Lyer illusion has been used to test pointing and grasping [6,20,21]. It has generally been found to have smaller effects on actions than on perceptual judgments.

that the Titchener size-contrast illusion (Fig. 1a) affected perceptual judgments to a significantly greater extent than it affected the maximum grip aperture in grasping [1]. Several other reports supported the idea that actions were relatively immune to illusions [2–8]. In a recent article in TICS, Carey [22] reviewed several studies of illusions and action and concluded that these studies were generally consistent with the perception–action model. However, a number of findings seem to be inconsistent with this conclusion [9–21], as I discuss below.

A second model of illusion effects on action emphasizes task demands. This model posits that illusions tend to affect perceptions more than actions because of the particular nature of the tasks used to represent perception and action [9–12]. One version of the tasks-demands model (the 'absolute–relative' version) was recently put forward by Bruno [23]. According to this model, the 'action' tasks given to participants generally require the use of absolute frames of reference. This means that the visual input used in these tasks involves aspects of visual information that are focused on the target and are independent of the visual context, and therefore not susceptible to many visual illusions. Conversely, processes likely to be used in 'perception' tasks generally depend on contextual visual information that is susceptible to illusion effects.

A study conducted by Vishton *et al.* [9] examined whether it was the use of a relative or absolute reference frame that resulted in large effects of the horizontal–vertical illusion on performance. Vishton *et al.* observed that a three-fingered 'grasp' of a two-dimensional triangular figure (Fig. 1b) was susceptible to the horizontal–vertical illusion. This suggested that illusions could affect actions if participants were encouraged to use a relative frame of reference, such as in multi-digit grasping.

I am not entirely convinced by Vishton et al.'s results, however. For one, it could be argued that movements directed towards 2-D figures are not programmed and executed in the same way as movements directed towards 3-D objects [29,30]. For another, Vishton et al.'s study assumes that people normally equalize the distance between the index and middle fingers and thumb, when grasping triangular-shaped objects, something I consider doubtful. A way to address this issue would be to include a condition in which the triangular object was rotated 90 degrees. If the absolute-relative model were correct, then the illusion should then result in a relative increase in the distance between the index and middle fingers compared with the thumb, rather than the relative decrease found by Vishton et al.

A third model of illusion effects on action is what I will here call the 'common-representation' model [13–15], recently hinted at by Franz [24]. The common-representation model contends that perception and action access a common visual representation that is susceptible to illusions. In this model, the apparently small illusion effects on action are a consequence of the methods used in many illusion studies. These methods, it is argued, are often biased towards underestimating illusion effects on perceptions.

Franz *et al.* [13,14] and Pavani *et al.* [15] reasoned that the perception and action tasks used in the Aglioti *et al.* [1] study were flawed in that only the perception task required participants to attend to both parts of the Titchener illusion simultaneously. Conversely, when the grasping task was performed attention needed only be paid to one of the Titchener displays at a time. This method might have biased the illusion effect on grasping to be smaller than its effect on perception because

#### Box 1. Is on-line control special?

Most of the apparent dissociations between perception and action are dependent on corrections that are made on-line, and are reflected in indices of action occurring late in a movement. By contrast, there appears to be little evidence that the information used during action planning is much different from the information used during perception. Is there reason to suspect that on-line control is what really distinguishes action from perception? The following observations make the case for on-line control.

- Targets that moved during a saccade were consciously perceived as stationary, yet pointing movements were adjusted to the new location of these targets on-line, and without vision of the hand [a].
- On-line adjustments to a target that changed position in accordance with reach onset preceded conscious awareness of the perturbation by as much as 150 ms [b].
- On-line adjustments in the shape of the hand to a change in the size of a target
  occurred even when the change was too small to be noticed consciously [c].
- A patient with optic ataxia was impaired at making on-line adjustments to target perturbations, although her movements to stationary targets were within the same range of accuracy as healthy controls. This suggested that her deficit was specific to on-line control [d].
- Transcranial magnetic stimulation applied over the intraparietal sulcus disrupts on-line adjustments to perturbed targets, but has no effect on movements to stationary targets [e].

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the visual effect of the illusion would be expected to be larger when both displays must be attended to than when only one display must be attended to. By modifying the experimental design, both Franz *et al.* [13] and Pavani *et al.* [15] found that when the two tasks were matched in attentional requirements, participants were equally affected by the Titchener illusion in the perception and grasping tasks.

There is, however, a difficulty with the common-representation model in that most other experiments involving illusions and action have adequately matched the attentional requirements of the two tasks [2-5,7,12,13,15-19], but still the perceptual effects of illusions have often been dissociable from their effects on action. Franz and Pavani countered this argument by raising doubts over the methods used in many perception tasks, even when the attentional requirements were matched. For example, they contended that indicating a target's size by matching it with the thumb and forefinger [2,5,21] tends to lead to inflated estimates of illusion effects and, for the studies reviewed by Franz [24], this did appear to be the case. More generally, I would contend that it is inherently difficult to quantify and compare effects of illusions on the many different behaviors that have been used to measure perception and action.

### The planning-control model

Peter Dixon and I have argued that illusion effects on action can best be explained by a model that supposes the existence of separate visual representations in the planning and control of actions [16–19]. The 'planning–control' model suggests that what have generally been viewed as dissociations between perception and action might more accurately be described as dissociations between perception and on-line control (see Box 1).

The origins of the planning–control model date back more than a century, to Woodworth [31], who claimed that movements were composed of an 'initial impulse' stage and a 'current control' stage. Over the years this model has been much examined and extended [32–34]. Our version of the planning–control distinction adds to these earlier theories by positing that independent visual representations subserve each stage of action [16–19].

In regard to the illusion and action debate, the planning-control model predicts that illusions induced by the context will affect only planning and not control. The rationale for this is that planning must account for the context surrounding a target. This is necessary not only to select the target from a number of potential targets in the first place, but also because non-target objects often act as obstacles that must be avoided. However necessary the inclusion of the context in the planning phase, this can also result in errors in planning that occur when the context induces a visual illusion [35].

Errors in the plan caused by illusions are of little consequence to the overall success of the movement, however, because these errors can be corrected in flight by the control system. The control system monitors and corrects movements using an independent visual representation. This representation provides a finegrained analysis of the spatial characteristics (i.e. size, shape, orientation) of the target, independent of the context. The focus on the target alone by the control system explains why contextual objects are given a relatively wide margin by planning [36], as control cannot easily switch attention to these objects in flight.

Control makes use of several sources of information, including visual and proprioceptive feedback, an efference copy (a 'blueprint' of the movement plan forwarded from motor planning centers), and visual information stored in the control representation. Removing one or more of these sources of information has consequences for the ability of the control system to correct movements. For example, delays of more than 2 s between removal of the visual stimulus and movement initiation result in a complete decay of the control representation, and so illusion effects on these movements will not be corrected on-line [6,7,21].

The dynamic illusion effect in reaching One criticism of studies of illusion and action is that almost all the experiments have used only a single index of action, for example, the maximum grip aperture [1,2,7,13–15], or the accuracy of pointing movements [4,6]. In studies such as these, the index of action occurs late in the movement. Maximum grip aperture typically occurs at a time between 65–75% of movement duration; pointing accuracy is normally assessed as where the finger or pointer ends up (i.e. at 100% of movement duration). Using such measures allows ample time in which illusion effects on planning could have been corrected on-line. For example, when perturbations of a target's size or position are introduced, adjustments in the trajectory or the grasp occur extremely quickly, often within 100 ms for arm trajectory [37], and 175 ms for grip scaling [38].

We therefore addressed the possibility that illusion effects on planning might be corrected on-line. We did so by taking continuous measures of action over the course of reaching and grasping movements. In one set of studies, a tilt illusion was used as participants reached out to grasp a bar (Fig. 1c). When the effect of the illusion on the orientation of the hand was measured over time, the illusion in fact had a large effect early in the movement, but a continuously decreasing effect as the movement progressed [16–18]. By the time the hand reached the bar, the illusion effect was almost eliminated, allowing participants to grasp the bar without difficulty.

Another study extended this method to the Titchener illusion [19]. Here, we measured the grip aperture throughout the movement rather than just at its maximum. We found that the Titchener illusion had a large effect on grip aperture early in the movement, but that this effect declined as the hand approached the target.

Two studies by Westwood and his colleagues also took kinematic measures that were temporally separated. Westwood *et al.* observed that the Muller-Lyer illusion (Fig. 1d) had larger effects on kinematic markers that occurred in the first half of the movements (peak grip velocity, peak wrist velocity) than on markers that occurred in the second half of the movements (maximum grip aperture) [20,21].

Other models' explanations of the dynamic illusion effect Although the dynamic illusion effect and Westwood *et al.*'s results are consistent with the planning–control model, other models of illusion effects on action might also be able to explain them, although my sense is that in order to do so, these models would need to be somewhat extended. For example, a proponent of the perception–action model might explain dynamic illusion effects as resulting from an 'interaction' between perception and action modules. Such interactions would presumably take place during the transition between planning and control, with the perception module being involved in planning the movement and the action module being involved in controlling it. Similarly, a proponent of the task-demands model might argue that the planning and control of actions impose different demands on the motor system, resulting in context (i.e. illusion) effects being larger earlier in the movement than later. Finally, proponents of the common-representation model might admit that certain components of on-line control are in fact less susceptible to visual illusions than perceptions, although they might note that large effects early in the movement are generally consistent with their model.

Criticisms of the planning-control model Although the planning-control model does well at explaining the effects of illusions on action, at least two potential difficulties of the model have been raised. For one, it is not intuitively obvious why movements made in open-loop conditions should show small illusion effects late in the movement [2,4-7,18-21]. One might suppose instead that the removal of visual feedback should eliminate on-line corrections. However, it has been shown many times that on-line corrections occur in the absence of visual feedback [39,40], including in our own studies of context-induced illusions and action [18,19]. It would appear then that corrections rely to a large extent on sources of information other than visual feedback, including stored visual information in the control representation, proprioceptive feedback, and efference copy.

A post hoc analysis by Danckert et al. also seems to pose difficulties for the planning/control model [8]. The original experiments in this debate were two conducted by Goodale and his colleagues that examined the effects of the Titchener illusion on grasping [2,5]. The re-analysis of these studies examined the effects of the illusion on the grip aperture over time. This re-analysis suggested that the illusion effects were never different from zero at any time during the movement, with the exception of a significant effect on the maximum grip aperture in one of the experiments [8]. These results contrasted with the results of our study, which showed a large early effect of the illusion that continuously declined over the course of the movement [19].

Danckert *et al.*'s analysis is clearly at odds with our results using the same illusion, although I think the inconsistencies could be due to two shortcomings of their analysis. First, whereas we scaled the illusion effects on grip aperture by the corresponding effects of disc size on grip aperture ([19]; see also [13–18]), Danckert *et al.* did not. Such scaling is necessary because a 'small' illusion effect early in the reach (when the slope of the relationship between grip aperture and actual disc size tends to be very small) actually represents a much greater impact of the illusion on grasping than a similar effect later in the reach (when the slope approaches 1.0). Second, the data in the Danckert *et al.* analysis were Conclusions

considerably more variable than in our study using the Titchener illusion, and it is not clear whether their experiments had sufficient power to detect illusion effects, assuming the appropriate scaling had been done.

Given what I feel are two fairly considerable shortcomings of the Danckert *et al.* analysis, I am hesitant to accept their results. On the other hand, should these issues be addressed in future studies, I would be interested to see the results of this and other analyses of illusion effects over time. Such analyses could go a long way towards fully understanding the dynamic illusion effect.

The question of how and when visual illusions affect

planning-control model is but one of a number of

possible explanations for illusion effects on action.

With regard to the dynamic illusion effect, I believe

that the planning-control model provides a simple

task-demands, or common-representation models.

account that is not rivaled by the perception-action,

actions is far from settled. Indeed, the

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#### Questions for future research

- Do different illusions exert different effects on perception and action, and if so, why?
- If the visual information required for grasping an object were degraded, what impact would this have on illusion effects on action?
- What impact would introducing delays have on the dynamic illusion effect?
- Under what circumstances is binocular vision an advantage in reaching to targets that are susceptible to visual illusions?
- What regions of the brain might be important in limiting or correcting illusion effects on action?

Future research on illusion effects over time will inform us further about the interaction between vision and motor control. My sense is that this is just one of many lines of research on illusions and action that will help improve our understanding of the transformations that take place between visual input and motor output.

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