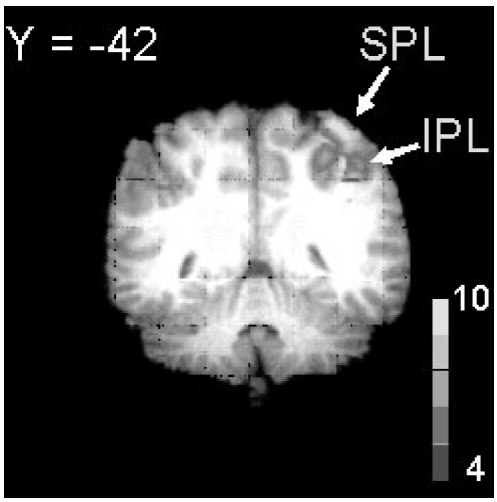


Figure 1 (Vaillancourt et al.). Visuomotor Process in IPL and SPL. The group functional map was obtained from a group Fisher test of the force with visual feedback minus rest t-map across the ten subjects. The group map was overlaid on a single subject's Talairach transformed brain. The image is shown from a radiological perspective.

under the control process – and include the activation of the superior parietal lobule and the cerebellum. However, the findings from that study demonstrate that the control process may also occur in the inferior parietal lobule. Although not depicted in Figure 1, a distributed network within the anterior prefrontal cortex, premotor cortex, putamen, lateral cerebellum, intermediate cerebellum, and the dentate nucleus assisted the parietal lobules in regulating the on-line visual control of force.

The implications from the work in PD and the findings from the neuroimaging studies lead us to two possible conclusions: (1) that Glover's control process occurs in a more widely distributed network that includes multiple cortical and subcortical regions; or (2) that the on-line visual control of the force task includes a planning component not recognized within Glover's theoretical framework. To reconcile these differences we turn to a postulated model of the visual control of force that may support the latter conclusion.

Slifkin and colleagues (2000) examined the influence of intermittent visual feedback on the variability and frequency of continuous force production. During the force task, subjects received visual feedback at different frequencies that were presented at intervals as slow as every 5 sec to as fast as every .04 sec. Slifkin and colleagues found that there was a hyperbolic reduction in the dominant frequency of force output at 1–2 Hz, reaching asymptotic values near a visual feedback frequency of 6.4 Hz (or 150 msec). Slifkin et al. proposed a model where force error is accumulated at a maximum frequency of 6.4 Hz. Each successive force error is then held in short-term storage (with a maximum temporal capacity of 1–2 sec (Elliott & Madalena 1987; Vaillancourt & Russell 2002), and, after approximately one second, an error correction signal is computed. In the context of Glover's theory and the Slifkin et al. model of continuous force production, the control process would operate at a fast time scale where the maximum is 6.4 Hz, and the planning process computes the error signal about once per second.

In summary, the above explanation reconciles the apparent contradictory findings with Glover's postulated dichotomy of planning and control processes. While the proposed dichotomy of planning and control elegantly links historical models of Woodworth (1899) with theories of perception and action (Milner & Goodale 1993), the model does not account for the fact that the visuomotor feedback network extends into multiple cortical and subcortical regions (Vaillancourt et al. 2003).

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Further evidence for, and some against, a planning–control dissociation

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Abstract: We summarize a number of recent results from our own experiments as well as those from other laboratories. Some of these results support Glover's planning/control dissociation and some are at odds with it. We suggest that the model needs to be further refined and expanded.

In his target article, Glover has provided a welcome alternative theory for the evidence related to the perception-action/dorsal-ventral visual stream controversy. Like many new theories, it leads to more questions than answers, but this is not necessarily a bad thing, if it motivates those of us doing sensorimotor research to delve more deeply into the issues surrounding this controversy. Indeed, because Glover's planning–control dichotomy appears to map onto a circumscribed set of brain areas, it makes several predictions regarding activation patterns or the effects of lesions. For example, he suggests that transcranial magnetic stimulation (TMS) delivered to sensorimotor areas underlying planning or control should lead to corresponding deficits in these behaviors under appropriate conditions. A recent study from one of our labs has addressed this very question in the context of the perception-action debate (Lee & van Donkelaar 2002). Subjects were asked to point to the central circle in an Ebbinghaus display while TMS was delivered to either dorsal or ventral stream sites. Previously, we had shown that when the target circle appeared to be large, pointing movement times were shorter and velocities were greater than when the circle appeared to be small (van Donkelaar 1999). When TMS was delivered over either dorsal or ventral stream sites, this effect was significantly reduced. Interestingly, dorsal but not ventral stream stimulation also reduced the effects of target size even in a control condition without surrounding circles.

We interpreted these findings, taken together, to suggest that the dorsal stream contribution to the effect was mainly related to the motor aspects of the task, a conclusion that does not appear to differ drastically from Glover's point of view. A key issue with respect to his theory, however, is whether we were stimulating in the IPL or the SPL. According to the planning–control model, processing that occurs within the IPL is proposed to underlie the planning of the motor response and thus be susceptible to illusion effects. By contrast, SPL processing is thought to contribute to on-line control and to correct for any illusion effects induced during planning but to otherwise be immune to their influence. Therefore, according to the planning–control model, TMS over the IPL should significantly reduce the illusion effect because of a disruption of the planning process. By contrast, SPL stimulation should actually enhance the effect because of a disruption to the on-line control underlying the corrections in response to the illusion. Clearly, we observed the former result, which implies that we were in fact stimulating the IPL.

Localizing TMS sites is not the most exact science, but various clues can be used to make good approximations. For example, the site of stimulation in our study was 7 cm posterior to the motor hot point. By comparison, in a study by Desmurget and colleagues (1999) examining the effects of TMS on on-line corrections within

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the posterior parietal cortex (PPC), a site 4 cm posterior and 0.5 cm medial to the motor hot point was stimulated. This difference in the relative locations of the stimulation sites in the two studies and the typical underlying layout of the intraparietal region suggest that we were in fact affecting IPL processing. The results from our TMS study therefore appear to be consistent with Glover's planning–control model.

More generally, however, we feel that Glover's theory does not place enough emphasis on the contributions to planning and control from areas such as the premotor cortex, supplementary motor area, and motor cortex. There is a tendency in the target article to focus on the functional distinctions between the SPL and IPL, with only a limited discussion of some of the areas to which these dorsal stream sites project. Indeed, perhaps a more appropriate approach is to think of planning/decision-making as a parietal-prefrontal process and control/execution as a motor area process with an evolution from planning to control as one moves from input to output areas. For example, one criterion for control/execution should be the ability to elicit responses by direct stimulation. This definitely holds for motor areas such as the motor and premotor cortex, and (for eye movements) the frontal eye fields and superior colliculus. Moreover, there is clear evidence that control processes can occur within the motor cortex. In particular, Desmurget and colleagues (2001) have used brain imaging to demonstrate that the motor cortex (along with the cerebellum and PPC) is activated specifically during the on-line control of reaching movements. It would therefore seem that control can occur at even fairly low levels in the sensorimotor system. We think that it is vital to expand the model to include the contributions from these levels to the control process.

Finally, although Glover explicitly states that the planning–control model is not meant to generalize to eye movements, we feel that the well-documented relationships between hand and eye movements can provide further insights with which to judge the model. For example, Glover uses the results of a study on the Roelofs illusion (Bridgeman et al. 1997) as evidence for his planning–control model of reaching – while the illusion does affect movements to remembered targets, movements with no delay are presumably corrected through on-line control so that the illusion's effect on planning is eliminated. However, recent work here (Dassonville & Bala 2002) demonstrates that saccadic eye movements show the exact same pattern of accurate and inaccurate localizations for immediate and remembered saccades, respectively. Given the ballistic nature of saccades, though, on-line control cannot be used in an analogous way to explain the lack of illusory effects for immediate saccadic responses. It follows that either the saccadic system uses an altogether different mechanism to overcome the illusion than does the manual motor system, or that they both use a single mechanism that is not based on a planning–control distinction – to us, the latter possibility seems more parsimonious. Thus, a better understanding of the relations between eye and hand under illusory conditions (e.g., Binsted & Elliot 1999) will undoubtedly provide further insight into this issue. For now, though, it seems that the jury is still out.

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Human vision focuses on information relevant to a task, to the detriment of information that is not relevant

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Abstract: Glover offers an account for why some pictorial illusions influence early but not late phases of an action. His proposed corrective control process, however, functions normally in the absence of continuous visual information, suggesting that the stimulus is registered veridically prior to action onset. Here I consider an alternative account, based on differing informational constraints of behaviors (and phases of behaviors).

Glover's planning-versus-control (PVC) model provides an intriguing explanation as to why pictorial illusions affect some behaviors much more than others. Earlier theories, most notably the Milner and Goodale (1995) perception-versus-action (PVA) model, have described the presence of separate visual streams for "perception" and "action," and acknowledged that the two streams must, of course, interact with one another. However, the form of that interaction has been only vaguely described. The PVC approach takes on the important task of describing the details of this interactive process.

The PVA model could be extended in some straightforward ways to account for most of the findings reviewed by Glover, if one simply presumes that the "perception" stream is involved in planning and early execution of actions, and the "action" stream controls the final stages of a behavior. This tremendous flexibility of the PVA theory, however, is one of its great limitations. The PVC model makes far more precise predictions – predictions that could potentially be refuted by further experimentation because of their specificity. Only by increasing the precision of our models do we make progress toward developing a better understanding of human perception and action.

With these strengths in mind, there are some decided limitations to the PVC approach that should be noted in the realm of size-mediated judgment versus reaching, described in much detail in this commentary. As Glover summarizes, it is generally believed that pictorial illusions exert large effects on (a) judgments and the early stages of visuomotor actions, while exerting small or nonsignificant effects on (b) the latter portions of a visuomotor action. The PVC approach claims that the planning of a reaching action is strongly influenced by pictorial illusions, and a corrective control process removes that error during the course of the reach. Implied by this theory is a closed-loop action control process that uses information from a "quickly updated visual representation in the SPL, coupled with visual and proprioceptive feedback, and an efference copy of the movement plan" (sect. 1.1, para. 2). Glover later states, "Put simply, the control system is focused on the on-line correction of the spatial parameters of the action" (sect. 1.1.3, para. 6).

One property of visuomotor actions from Glover's own studies, however, does not fit well with this story. Even when the view of the stimulus is removed at the onset of the action, the corrective process proceeds normally, just as when the stimulus is fully visible. Glover specifically states that the "dynamic illusion effects" are apparent when vision of the hand and target are blocked during the reach (Glover & Dixon 2001c; 2002a). If the control system operates by providing on-line corrections to the process, then having visual information available on which to base the correction should be important. The fact that it is not suggests that the information for fully specifying the action, including the correction, is available before the action begins, that is, during the planning phase.

My collaborators and I have pursued an alternative account for the differences in the effects of pictorial illusions on judgment versus reaching behaviors based on the differences in the informational demands of the tasks (Vishton & Fabre 2003; Vishton et al. 1999; submitted). For nearly all judgment tasks that have been

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