

nerod 1986; Jeannerod et al. 1994; Perenin & Vighetto 1983; 1988). Damage to the SPL can also result in an absence of on-line corrections to perturbed targets (Pisella et al. 2000). The patient D.F., with damage in the ventral stream, exhibits some planning deficits, but relatively intact on-line control (Carey et al. 1996; Goodale et al. 1994b; Milner et al. 1991; Milner & Goodale 1995).

Although I have outlined a collection of regions associated with both the IPL and planning, on the one hand, and the SPL and control, on the other, future studies will be needed to clarify and elucidate the roles of these allied regions in their respective stages. Methods such as fMRI and TMS, coupled with innovative behavioral and neuropsychological studies, should offer excellent chances for isolating and examining the respective neural and behavioral bases of the planning and control of actions.

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## Open Peer Commentary

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### fMRI evidence for and behavioral evidence against the planning–control model

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**Abstract:** Consistent with the planning–control model, recent fMRI data reveal that the inferior parietal lobe, the frontal lobes, and the basal ganglia are involved in motor planning. Inconsistent with the planning–control model, however, recent behavioral data reveal a spatial repulsion effect, indicating that the visual context surrounding the target can sometimes influence the on-line control of goal-directed action.

Glover's planning–control model postulates distinct brain areas mediating planning and on-line control of action. In this view, planning involves the inferior parietal lobe, the frontal lobes, and basal ganglia, whereas control involves the superior parietal lobe and the cerebellum. In support of this distinction, Glover cites several neuroimaging studies that used PET. Recently, we completed an fMRI study that was specifically designed to study the neural mechanisms of motor planning (Adam et al. 2003). Importantly, this study used the finger-precuing task (Miller 1982) to measure motor planning. The finger-precuing task requires subjects to respond to spatial-location stimuli with discrete re-

sponses from index and middle fingers of both hands. Preceding the target stimulus, a spatial precue indicates a subset of possible finger responses; this allows the selection and preparation of two finger responses. The fMRI data revealed that the preparation of discrete finger responses was associated with increased activation levels in the parietal cortex (inferior and superior regions, intraparietal sulcus), the frontal cortex (middle frontal gyrus, premotor and supplementary motor cortex), and the basal ganglia (caudate nucleus and putamen). This outcome generally corroborates the planning network as proposed by Glover, except for the involvement of superior parietal lobe (and possibly the intraparietal sulcus bordering the inferior and superior parietal lobe). However, as Glover has pointed out, and consistent with other neuroimaging studies, the increased activity in the superior parietal lobe probably reflects the attentional effects of the spatial cues.

Furthermore, the planning–control framework introduced by Glover postulates a distinction between planning and on-line control of actions. Whereas planning is assumed to take into account various sources of visual and cognitive information, control is limited to the spatial characteristics of the target and the actor. Importantly, according to the planning–control model, the visual context (e.g., objects surrounding the target) is ignored during on-line control. However, recent data suggest that the visual context also can influence control. In two studies (Keulen et al. 2002; 2003), we investigated distractor interference in selective reaching. Participants pointed to a target appearing in isolation or concurrently with a distractor. The distractor could appear either in front of or beyond the target. With a small (i.e., 5 mm) separation between target and distractor we observed a spatial repulsion effect; that is, the movement endpoints were biased away from the location of the distractor. In other words, participants ended their movements within the prescribed target area so as to maximize the distance to the adjacent distractor (for a first demonstration of this effect, see Fischer & Adam 2001). The fact that the repulsion effect was small but consistent (i.e., 0.6 mm on average), and occurred only when target and distractor were close to each other, suggests that the spatial repulsion effect reflects on-line control rather than planning. Thus, the spatial repulsion effect indicates that the immediate visual context surrounding the target can influence the on-line control of actions. Certainly, this observation is not fatal for Glover's model, but it represents a minor qualification to one of its premises.

### At least some electrophysiological and behavioural data cannot be reconciled with the planning–control model

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**Abstract:** The planning/control distinction is an important tool in the study of sensorimotor transformations. However, published data from our laboratories suggest that, contrary to what is predicted by the proposed model, (1) structures in the superior parietal lobe of both monkeys and humans can be involved in movement planning; and (2) fast pointing actions can be immune to visual illusions even if they are performed without visual feedback. The planning–control model as proposed by Glover is almost certainly too schematic.

Can we make a sharp distinction between planning and control in human action production? There is little doubt that planning must precede the onset of movement, whereas on-line control must become increasingly important as the action progresses. It remains to be seen, however, whether this obvious temporal ordering is

also implemented in separate neural structures running on the basis of different internal representations. Although Glover's model is remarkably successful in accounting for a large body of data, it seems to us that other results remain problematic in the light of a sharp planning/control distinction.

One of us (Battaglini) has described arm-movement related neurons in area V6A of the macaque superior parietal lobe (SPL). Comparing neural activity with arm electromyographic recordings clearly showed that several of these neurons discharged prior to the onset of movement (Galletti et al. 1997b). Further analyses suggested that as many as 30% of these V6A neurons may be activated before the onset of a reaching movement (Fattori et al. 2001). In a lesion study, small bilateral lesions in the same area (V6A) of the green monkey produced deficits in fast, ballistic reaching and grasping. When presented with food (raisins) at specific egocentric distances, in initial trials, lesioned monkeys misreached the targets several times and only in later trials reached correctly from the start. Moreover, lesioned monkeys failed to generalize their training to other egocentric distances, as one would expect if they suffered from a planning deficit (Battaglini et al. 2002a; 2003). Contrary to Glover's predictions for humans, these data suggest that the monkey SPL may be involved in both planning and control. Although these results may reflect functional differences between the human and monkey brain structures (but see Galletti et al. 1997a), in EEG studies of reaching in humans Battaglini also found a clear activation at the SPL before the onset of movement (Battaglini et al. 2002b). These findings suggest that Glover's identification of the human SPL as the site of on-line control may be too schematic.

Similarly, human studies from the second of our laboratories (Bruno) may be interpreted as evidence that Glover's conception of the internal representations used by planning and control is also too schematic. In a study of bimanual, fast reaching to the endpoints of a surface subjected to Kanizsa's compression illusion (Bruno & Bernardis 2002), Bruno measured performance in two motor conditions. In the first of these conditions, blindfolded actors extended their arms until their hands were in the position where they had seen the endpoint of the surface. Results showed no hints of compression, although visual discrimination data showed the usual 5% compression reported in previous studies (Kanizsa 1975). Given that these actions were performed quickly and without visual feedback, in the planning-control framework they should have reflected a greater influence of the "cognitive" representations used for planning. However, the results failed to show the "cognitive" effect of the illusion. Even more convincingly, in a second condition actors simply placed their hand in front of their chest, in spatial alignment with the surface endpoint, without extending their arms completely. Given that this second action corresponded to the early part of bimanual reaching, in the planning-control framework it should have reflected an even greater influence of the cognitive representation. However, the results again failed to show any cognitive effect. In fact, there was no difference with the full reaching condition. Comparable results were found in a pointing study, which also generalized them to a variant of Müller-Lyer's illusion (Bruno & Bernardis 2003).

## Can the motor system utilize a stored representation to control movement?

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**Abstract:** This commentary focuses on issues related to Glover's suppositions regarding the information available to the on-line control system and the behavioral consequences of (visual) information disruption. According to the author, a "highly accurate," yet temporally unstable, visual representation of peripersonal space is available for real-time trajectory corrections. However, no direct evidence is currently available to support the position.

Glover's planning-control model (PCM) suggests that an unfolding visual representation (of the aiming environment) gradually assumes control of goal-directed action. Certainly, this view is consistent with a number of investigations suggesting that "control" builds throughout the time-course of visually-guided movements, culminating in a smooth transition between preplanned and on-line control processes (Elliott et al. 1999; Heath et al. 1998). But what happens to on-line control processes when vision of the aiming environment is occluded at some point prior to the movement (i.e., so-called memory-guided reaching movements)? Glover's PCM assumes that a visual representation persists and is available to the motor system to rapidly modify the *memory-guided* reaching trajectory. Because this visual representation is assumed to be transient in nature, delays of greater than two seconds purportedly lead to near-complete decay of the visual representation, resulting in an action executed *without the benefit of on-line control*. The inference here is that a stored visual representation may serve as a valid, albeit temporally unstable, spatial referent for executing (error-nullifying) corrections to the movement (<2-seconds delay). Undoubtedly, this account of the PCM is rooted in Elliott and Madalena's (1987) position that "highly accurate" sensory information about the aiming environment is available for "on-line error reduction during the movement." Specifically, Glover suggests that:

movements made after delays much longer than two seconds will be executed entirely 'as planned' (i.e., without the benefit of on-line control). (target article, sect. 1.1.3, para. 5)

The notion that a stored, visual representation of the aiming environment is available for "on-line error reduction" represents an intriguing possibility; we wonder, however, whether there is empirical evidence to support this view. Indeed, our examination of the memory-guided reaching literature indicated that it is largely unclear whether stored visual information about the aiming environment is used for movement planning, on-line movement control, or both. This primarily reflects a limitation of previous work and emphasis on the endpoint characteristics of memory-guided reaches (e.g., Elliott 1988; Elliott & Madalena 1987; Westwood et al. 2001a; 2003); no direct evidence (i.e., movement corrections or kinematics) is available to support the position that stored target information is used for on-line movement control following brief delays. Hence, the reported residual accuracy of memory-guided reaches might simply reflect the use of a stored representation of the aiming environment for movement planning processes; that is, stored information is not used for error-nullifying limb/target corrections – regardless of the length of the memory delay (Flanders et al. 1992; Plamondon 1995).

In an attempt to reconcile this issue, we (Heath & Binsted 2003), present very recent data in which participants (N=15) completed a number of reaching movements (450) to three mid-line targets (20, 30, 40 cm) in three visual conditions: a visually-guided one and two delay intervals (0 and 5 seconds of delay, respectively). To infer movement control, we implemented a