of a single, more complex process, rather than being two independent processes.

Glover's model also seems to depend on the *locality assumption* – the position that planning and control processes (in this case) are independently implemented in two distinct brain areas, the IPL and SPL, respectively. According to this assumption (and central to Glover's model), damage to one of those brain areas will produce a discrete impairment that can be identified with and circumscribed to the affected module without affecting critically the workings of the remaining components of the system (Farah 1994). The IPL and SPL, however, are believed to be part of the fronto-parietal network, which functions as an integrated system during the execution of movements (Wise et al. 1997). Glover's use of neuropsychological evidence to support the planning–control model relies on the locality assumption. Glover assumes that local damage to the brain produces only a selective behavioral impairment, which can be identified with the malfunction of a distinct cognitive process. It is one thing to assume the independence of the brain centers putatively responsible for planning and control, but it is another to assume that the planning and control processes are thus *necessarily* independent (Farah 1994). The functional distinctions drawn on the basis of anatomical evidence artificially reduces the complexity of movement control to a dichotomy in the planning–control model, even though the brain system responsible for the execution of reaching-grasping is believed to be distributed among a complex network of connections linking different brain centers (Ietswaart et al. 2001).

Glover presents a host of neuropsychological case studies to support his planning–control model. His strategy is one of establishing a double dissociation: Damage to the IPL disrupts planning, but not control, and damage to the SPL disrupts control, but not planning. That double dissociation is supposed to provide evidence that planning and control reflect the activity of independent neurocognitive modules, respectively located in the IPL and SPL. But the argument for the existence of independent neurocognitive modules for planning and control based on double dissociations entails a circular reasoning (see Shallice 1988) – double dissociations are assumed to occur only in the case of modular architectures, and therefore cannot be used to verify the existence of neurocognitive modules (Van Orden et al. 2001).

In addition, Glover explicitly states that the neuropsychological evidence he provides is inconsistent and in some cases may fit the alternative model (perception–action) as well as the planning–control model. Nevertheless, that evidence is included because of its parallels with the results of PET studies. The taxonomy of cases used is strongly reminiscent of the classical model proposed by Liepmann (1900), even though Liepmann's model and the line of reasoning introduced by it are recognized as an oversimplification (Cubelli et al. 2000). This is not an innocent fact, given the similarities between Glover's and Liepmann's models. (Liepmann's model stresses the importance of the division between two separate stages in the production of movement: the formulation of a motor plan – planning, in this case – and the implementation of the planned spatio-temporal sequence of movements – control, in this case.) The argument for the existence of representations or memories of movement is a critical point of discussion in the neuropsychological literature; it is conceived by some authors as a bottleneck in the study of apraxia (Iestwaart et al. 2001).

We feel that Glover's model is constrained by the assumptions of neurocognitive modularity and locality, while the experimental evidence is either inconsistent with these assumptions (e.g., parameter crossover), or inconclusive with respect to them (e.g., the neuropsychological case studies). These assumptions have been criticized by several authors (e.g., Farah 1994; Uttal, 1998; 2000; Van Orden et al. 2001; Weldon 1999) and seem, in this case, to lead us down the wrong path in our efforts to understand movement control.

Is efficient control of visually guided movement directly mediated by current feedback?

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Abstract: The main issue addressed here concerns the central notion of a forward internal model, through which efficient control and planning are linked together and to the related online predictive error processing. The existence of such a model has strong implications in action production and may question Glover's model.

Glover's approach to hand-reaching follows a view current since Woodworth (1899), Fitts (1957), Keele and Posner (1968), and Meyer et al. (1988), according to which the movement results from two basic components: one planned action determining the gross organization of the response and a final part including a fine control of the hand movements based on the simultaneous vision of the hand and target (in Glover's model, supposed to involve, respectively, the IPL and SPL). The extent to which visually guided movements are planned in advance or controlled on-line during the execution, is still a matter of debate. Whereas many studies have searched for the origin of planning errors (see Desmurget et al. [1998] for a review), another series of experiments have tried to identify whether the so-called planning phase was really planned and not under the control of either central or peripheral feedback. These studies have been carried out in normal subjects (Bridgeman et al. 1979; Desmurget et al. 1999; 2001; Goodale et al. 1986; Pélisson et al. 1986; Prablanc & Martin 1992), but also in deafferented patients (i.e., those who have lost the sense of position) (Bard et al. 1999). Basically, their overall finding is that a third component does exist, namely, an unconscious control applied during the first phase of the movement. In all these experiments, a target perturbation inducing a planning error was randomly introduced during the so-called saccadic suppression, making these perturbations unconsciously perceived. The specificity of the corresponding corrections was both their smoothness and their early stage as compared with the corrections observed under conscious double step experiments. In these latter experiments, despite sometimes a nonspecific early short reaction time, the path deviation indicating the corrections occurred with a normal reaction time, and with a clear double peak velocity profile (Georgopoulos et al 1981, Soechting & Lacquaniti 1983). One important point to notice is that the smooth online corrections were mostly observed for unconsciously detected errors. In Glover's planning–control model, online adjustments to perturbations of the spatial characteristics of the target should occur relatively quickly, irrespective of the nature of the perturbation.

However, this unconscious error detection may not be the only prerequisite for producing fast and smooth corrections. The delays introduced by conduction processing times at the different relays along the visuomotor stream have led some authors to postulate the existence of a "look-ahead" or Smith predictor (Hoff & Arbib 1992, Miall et al. 1993). More recently, Desmurget and Grafton (2000) have emitted the hypothesis that the correct execution of a hand movement is based mainly upon a forward internal model. This "internal model" is a predicted output of the upper limb endpoint derived from the real command signals fed to the motor apparatus, together with the updated passive visual and proprioceptive information of the end-point effector (the hand). In another paper, Prablanc et al. (2003) have also suggested that the fast error correction was not directly derived from the available retinal error signal between hand and target, but resulted from a comparison between a central representation of both the target and hand, mixing both sensory signals (visual and proprioceptive) and an efferent copy of the upper limb motor commands. According to Desmurget and Grafton (2000), if the normal vision of the hand and target is available during the motor response, the

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detected errors should not be taken into account by the control system, whereas Glover's planning–control model should cope with these error signals irrespective of the existence of a correct or biased internal model.

We present the paradigm in brief here. A way to unexpectedly bias the internal model is to introduce a random shift in the initialization of the model by the most efficient inflow signal (i.e., vision of the hand and fingers in their resting state) (Revol et al. 2003). Although the initial position of the endpoint effector is defined through multisensory cues such as vision and proprioception, the weight of the former is high enough to create a bias when viewing the hand through prisms goggles. Pointing performance of control subjects were thus compared: (1) when an erroneous planning together with a biased internal model occurred (using left or right prisms to displace the initial vision of the hand); or (2) when a planning error was induced by a small target displacement throughout the saccadic suppression while the internal model remained intact. When an initially displaced vision of the hand occurred, pointing became inaccurate showing an incapability to correct the erroneous planning despite the undistorted target position and the natural visual reafferences from the moving limb. In contrast, a similar planning error induced by an intrasaccadic target jump was unconsciously corrected despite the lack of visual reafferences of the moving limb. These results are hardly compatible with Glover's planning–control theory. Rather, they fit the hypothesis that an intact internal model enables fast corrections as proposed by Desmurget and collaborators (Desmurget et al. 2001).

Glover refers to a possible generalisation of the planning–control model to the oculomotor system. In fact, the opposite should rather apply, as the most influential model of the saccadic oculomotor system since thirty years (Robinson 1975), relies on a single efference copy signal being used as a feedback signal to the saccadic controller, without any need for a visual feedback. The theoretical concept of a feedback taking into account both the efference copy of the multi-joint upper limb, and the visual and kinaesthetic reafferences and their underlying neural structures, had appeared much later, even very recently (Desmurget et al. 2001). However, one has to keep in mind that the simplicity of Robinson's saccadic model lies in the absence of a planning component: The whole saccade duration is devoted to control, whereas the control phase of Glover's model cannot operate properly without a subtle combination of coherent efferent and afferent signals reconstructing the instantaneous state of the moving limb, as explained above.

Another point raised by Glover's planning–control model is regarding the effect of illusion on movement. In contrast to the perception–action model (Milner & Goodale 1995), Glover's model suggests that only planning should be affected by the illusion of a surrounding context. Recently, Revol and Honoré (in preparation) asked control subjects to point, without any visual feedback, either at a central target or in the perceived direction of the same target under optokinetic stimulation. The pointing errors recorded were linked to the specificity of the pointing task, that is, only pointings performed at the target location were unaffected by visual illusion. These results fit neither Glover's model nor the action–perception model, but rather, suggest an action-perception gradient depending on the processing of the visual information (see Rossetti & Pisella 2002).

Parallel visual pathways from the retina to the visual cortex – how do they fit?

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Abstract: Which roles are played by subcortical pathways in models of cortical streams for visual processing? Through their thalamic relays, magnocellular (M) and parvocellular (P) projecting ganglion cells send complementary signals to V1, where their outputs are combined in several different ways. The synergic role of M and P cells in vision can be understood by estimating cell response entropy in all domains of interest.

The planning–control model proposed by Scott Glover in the target article, as well as the "what" versus "where" model of Ungerleider and Mishkin (1982) and the perception versus action model of Milner and Goodale (1995), all try to explain the roles played by the major streams of visual processing in the cerebral cortex. In these models, room must be left for the function of the subcortical visual pathways that feed the visual cortex with the essential information needed for their function. Originally, the magnocellular (M) and parvocellular (P) pathways were regarded as dedicated to specific visual functions, such as movement and visual acuity plus color vision. As such, many attempted to associate M and P activity to the functions of the dorsal and ventral cortical streams, respectively. This view was abandoned once it was demonstrated that the M and P signals mix largely inside V1; examination of the temporal and spatial requirements assigned to perception and action lent further support to this decision.

Visual information travels in a series of parallel pathways from the retina to V1. The M and P pathways are the best characterized (Silveira et al. 2003). They have their own set of bipolar cells that convey information to the M and P ganglion cells, which in turn project respectively to the magnocellular and parvocellular layers of the lateral geniculate nucleus (LGN). From there, the M and P relay thalamic neurons connected to specific V1 entrance layers. There are other ganglion cell classes connecting to the LGN koniocellular layers and pulvinar, from which visual information can reach V1 and other visual cortical areas (Hendry & Yoshioka 1994). These pathways remain separate until they reach V1 and then mix shortly after, as the information passes from V1 entrance layers to the other V1 compartments, and from the latter to the next visual cortical areas (Yoshioka et al. 1994).

All the models for visual cortical processing require the existence of multiple representations of the visual field, which are built either in egocentric coordinates or in coordinates centered with respect to the object (Milner & Goodale 1995). The information provided by the visual system is combined with a wide variety of nonvisual sensory and cognitive information to fulfill individual aims, including object perception, motor planning, and motor control. The visual information carried by light emanating from objects located in the ever-changing visual field has to be coded with enough precision in space and time to allow behavioral tasks to be adequately performed. However, because of the limits of quantum catch by the photoreceptor array, any gain in the capacity of locating an object in space more precisely is accompanied by a loss in the ability to measure precisely the moment of occurrence of a visual change, and vice versa (Land & Nilsson 2002). In addition, natural scenes are composed by singularities and periodicities, both in space and time, and the visual system has to have enough precision to evaluate not only spatiotemporal coordinates, but also their spatiotemporal frequency content. The simultaneous precision in time, temporal frequency, space, and spatial frequency is a general, basic problem in the design of measuring devices, and there is no way to increase the performance in all these domains at the same time (Gabor 1946; Silveira & de Mello 1998). All real devices, either natural or man-made, built to store, transmit, or analyze visual information, represent different degrees of compromise between precision in the space-

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