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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time domain and precision in the spatiotemporal frequency domain.

The uncertainty principle of Gabor (1946) establishes in a mathematical identity the impossibility of unlimited increase in the precision of measuring the time and temporal frequency of a phenomenon, $\Delta t \cdot \Delta f \geq 1/2$, where Δt and Δf represent the uncertainty in any measurement carried out simultaneously in the time and temporal frequency domains. The number of terms in this identity, called joint entropy in Gabor's information theory, can be expanded to accommodate the six dimensions of the retinal image or the eight dimensions of the visual field or the praxic field.

The visual coding required for perception of objects, motor planning, and motor control will vary with the function performed: No single brain representation of the space-time will fulfill all requirements. For instance, good spatial frequency discrimination can be critically important for some tasks, such as the recognition of a tree by its foliage; or precise representation of spatial coordinates might be essential to reach and grasp an object. Building a representation of the visual world adequate to the task to be performed is therefore essential to models like the planning–control model. This cannot be done by using a single retinal ganglion cell class to convey the information from the photoreceptor array to the visual cortex, because each retinal ganglion cell class is bound to a particular joint entropy combination. However, having two or more cell classes, such as the M and P cells, can solve the problem. What is needed is to combine their output in different ways in accordance with the task to be performed.

The synergic role of M and P cells in vision can be understood by estimating the cell response entropy in all domains of interest. For this, it is necessary to measure their impulse function in the domains of space and time, using discrete, localized stimuli. In addition, extended, periodic stimuli in the domains of spatial frequency and temporal frequency can be used to measure cell frequency response. The results are critically dependent on cell eccentricity; once M and P cell dendritic fields change dramatically with distance from fovea, it is hypothesized that all the functional properties would change accordingly. In addition, it has been shown that retinal illuminance also influences the response time course and receptive field size of retinal ganglion cells. The evidence so far indicates that the M and P cell responses differ in all domains, though displaying a considerable degree of overlap. The M and P cell properties in space and time, spatial frequency and temporal frequency, are complementary and result in different loci in Fourier space. Each pathway represents a particular trade-off to reduce joint entropy, and the visual system codes the spatiotemporal content of natural scenes more efficiently by using two or more channels having different entropy loci in the information diagram. M and P cells perform simultaneous and overlapping analyses of the visual field using different strategies to minimize entropy. This enables higher order visual neurons, similar to those of the dorsal and ventral cortical streams to combine M and P information in different ways and could explain why M and P outputs converge in the visual cortical pathways.

The requirements for perception, motor planning, and motor control are such that refined information about target location, time of occurrence of an event, and spatial and temporal frequency discrimination are needed in different degrees for each task. Each subcortical pathway conveys information with different degrees of precision in each dimension. The information is combined in V1 and sent to the different cortical streams as requested to build visual representations for perception and action. Each representation is a trade-off in the information space optimum for each task.

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The control process is represented in both the inferior and superior parietal lobules

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Abstract: Glover postulates that the inferior parietal lobule (IPL), along with the frontal lobes and basal ganglia, mediates planning, while the superior parietal lobule (SPL), coupled with motor processes in the cerebellum, regulates the control process. We demonstrate that the control process extends beyond the cerebellum and SPL into regions hypothesized to represent planning.

The target article by Scott Glover separates planning and control processes into distinct, separate representations spanning multiple cortical and subcortical networks. In particular, Glover argues that the planning process initiates and selects an adaptive motor program in the context of environmental and task goals, whereas the control process is focused on the on-line correction of the spatial parameters of the action. The specific thrust of Glover's thesis states that the inferior parietal lobule (IPL), along with the frontal lobes and basal ganglia, mediates planning, while the superior parietal lobule (SPL), coupled with motor processes in the cerebellum, regulates the control process. Two lines of empirical evidence suggest that this dichotomy may be too simplistic to completely understand the complex integrity of human brain function in the control of movement.

The first line of evidence is developed from research in patients with Parkinson's disease (PD). PD results from a loss of dopaminergic neurons in the substantia nigra pars compacta, leading to abnormal basal ganglia outflow from the substantia nigra pars reticulata and the internal segment of the globus pallidus to the thalamus (Albin et al. 1989; Wichmann & DeLong 1996). PD patients were shown to have more variable force output than age-matched healthy control subjects during a continuous grip force production task that required on-line visuomotor processes (Vaillancourt et al. 2001). Also, Ghilardi and colleagues (2000) found that movement kinematics and accuracy were similar between PD subjects and controls in the absence of visual feedback, but movements of individuals with PD had a shorter transport phase and reduced velocity compared with control subjects with on-line visual feedback. Direct neural recordings from primates have shown that a considerable number of globus pallidus neurons specifically respond to a visually-guided reaching task (Mushiake & Strick 1995). The findings on PD and the work from primate electrophysiology suggest that Glover's control process is associated with basal ganglia function – a region hypothesized by Glover to only mediate the planning process.

The second line of evidence comes from work in human neuroimaging. We conducted a whole brain echo-planar functional magnetic resonance imaging study at 3 Tesla (Vaillancourt et al. 2003), in which human subjects controlled continuous force output by grasping an apparatus with their middle finger and thumb. Subjects produced force at 15% of their maximum for 30 sec blocks while using on-line visual feedback, and rested by fixating on the visual target. Figure 1 depicts a group map of the significant activation found in the parietal cortex during the comparison of force with on-line visual feedback compared with rest. Both the inferior and superior parietal lobules were active bilaterally during the force control task. The task of producing force to the target required subjects to initiate the force, acquire the force target, and regulate force for the remainder of the 30 sec block. All subjects initiated force and acquired the target within 500 msec, and this time period was not included in the analysis shown in Figure 1. Only the force control period was included in Figure 1. According to Glover's definition, the task used in Figure 1 would fall

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