are friendly to this hypothesis (Desmurget & Grafton 2000; Desmurget et al. 1999), we believe that several key arguments put forward in the target article are debatable.

The first issue we would like to address is the ambiguity of the apparently obvious term *on-line control.* The "perturbation" paradigm illustrates this point: According to Glover, the pioneering experiment by Paulignan et al. (1991a) demonstrates the ability of the control system to accommodate a change in object location. When the kinematic characteristics of these changes are analyzed, however, it appears that the corrections are made, not by amending the current movement per se, but by aborting it and by replacing it by a new movement – that is, by re-planning a new response. In Paulignan et al.'s terms, the response to the perturbation "appeared to be composed of two submovements, the first one directed at the location of the initial target and the second one at the location of the new target." This type of "iterative correction" has also often been reported for movements directed at stationary targets (Meyer et al. 1988; Milner 1992). These corrections have been modeled using three different approaches, designated: (1) *Sequential,* in which the secondary movements are initiated at the end of the primary movement (Meyer et al. 1988). (2) *Overlapping,* in which the secondary movements are initiated before the end of the primary movement; the global motor response can then be characterized as a composite of several submovements overlapping with each others (Flash & Henis 1991; Milner 1992; Novak et al. 2002); (3) *Abort and replan,* in which the primary movement is aborted and replaced by a new movement when the error is detected (Massey et al. 1986; Paulignan et al. 1991a).

What is important here is that all these approaches rely on a similar observation, namely, that corrections are achieved by planning a secondary movement and adding it to the current one. This usage of the planning system to achieve movement corrections emphasizes the lack of clear distinction between control and planning, which raises questions about the validity of the strict division proposed by Glover in his model.

A second issue is the interpretation of several illusion experiments. In his article Glover refers, for example, to the study of Aglioti et al. (1995) to argue that illusions do not affect on-line control. A significant effect of the illusion on grip aperture was, however, observed in this study. The fact that this effect was less important than the perceptual estimate of the target size does not mean that it was not present and that it could be disregarded. In the same vein, Glover argues that visual feedback reduces illusion effects. It may be that the lack of effect under visual feedback lies in the fact that control is carried out, in this case, in allocentric coordinates. In other words, when vision is available toward the end of the movement, the correction is based on a retinal error signal that compares the state of the target directly with the state of the effector. This is what happens, for instance, when a subject wears small prisms and moves slow enough to allow feedback loops to operate: He reaches the target accurately without even being aware that he is wearing prisms (Guillaume et al. 2000). This point may explain the difference, emphasized by Glover, between the results published by Glover and Dixon (2001c) and those reported by Dyde and Milner (2002) in two similar studies involving the "tilt illusion": In the first study, the hand was visible during the last part of the movement and no effect of the illusion was reported; in the second study, vision of the hand was never available and an effect of the illusion was observed.

A third issue we want to stress is the existence of a specific contribution of the superior parietal lobe (SPL) to movement control and of the basal ganglia (BG) to movement planning. Regarding the SPL, imaging and patient data do not seem as clear as implied in the target article. In particular, two PET studies investigating the functional anatomy movement guidance have failed to reveal any specific contribution of the SPL. For visual feedback loops Inoue et al. (1998) reported a contribution of the inferior parietal lobe (supramarginal gyrus; Table 3). For nonvisual feedback loops, an activation was found over the intraparietal sulcus, but not within the SPL (Desmurget et al. 2001). In addition, it seems perilous to regard optic ataxia (OA) as a pure feedback-deficit on the basis of a single case study (Pisella et al. 2000). Clinicians often report that the hand goes "in the wrong direction from the beginning" in OA patients. In agreement with this claim we have shown, in a recent study, that the initial movement direction (a planning-related parameter) is affected in patients with OA (Desmurget et al., in preparation). Regarding BG, a direct link has recently been proposed between a deficit in on-line movement guidance and a dysfunction within the BG network (Lawrence 2000). The most convincing argument supporting this view was reported by Smith et al. (2000), who showed that patients with Huntington's Disease (in which early cell loss is restricted largely to the striatum) fail to correct for self-generated or externally imposed errors in movement trajectory. To explain this result, it was proposed that the sensory signal is biased when the BG are damaged, leading to an erroneous forward estimation of the motor state. Electrophysiological observations support this view by showing that passive limb movements activate the BG neurons (DeLong et al. 1985; Hamada et al. 1990) and generate abnormal (exaggerated) sensory responses in the pallidal neurons of Parkinsonian monkeys (Filion et al. 1988). This impaired responsiveness of the BG neurons to peripheral input could lead to an overestimation of the distance covered by the hand, and thus, hypometria (Klockgether et al. 1995).

How are cognition and movement control related to each other?

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Abstract: Our commentary focuses, first, on Glover's proposal that only motor planning is sensitive to cognitive aspects of the target object, whereas the on-line control is completely immune to them. We present behavioural data showing that movement phases traditionally (and by Glover) thought to be under on-line control, are also modulated by object cognitive aspects. Next, we present data showing that some aspects of cognition can be coded by means of movement planning. We propose a reformulation of Glover's theory to include both an influence of cognition on on-line movement control, and a mutual influence between motor planning and some aspects of cognition.

Glover proposes that motor planning and on-line motor control are two separate processes which follow two separate and independent visuo-motor pathways. In our opinion this seems too schematic, especially when behavioural and anatomic-functional data are taken into account.

Glover's first proposal is that motor planning is under the influence of a wide variety of visual (including spatial and nonspatial) and cognitive information, whereas on-line control is under the control of solely spatial characteristics of the target. This arises from both the assumption that the initial arm kinematics reflect movement planning and the findings that only the initial arm kinematics are affected by cognitive information. However, let us consider previous visual perturbation experiments (see, e.g., Gentilucci et al. 1992; Paulignan et al. 1991b). Corrections to visual perturbations occurred during the acceleration phase of arm movements (80–120 msec after perturbation). Because perceptual and/or cognitive information can lead planning into errors on target localization (see, for example, the illusion and the automatic-word-reading effects on arm movements), these should be quickly corrected (during the acceleration phase), if the on-line control is solely under the influence of the spatial characteristics of the target. Since this did not occur, it is possible that – at least in the initial movement phases – the on-line control is penetrable to cognitive aspects of the target object. Moreover, cognitive information affects the arm homing (deceleration) phase as well.

https://doi.org/10.1017/S0140525X04330025 Published online by Cambridge University Press

Marteniuk et al. (1987) showed that an effect of object fragility was also present in the last phase of arm movements (deceleration). We can therefore suppose that the final movement phase is planned as well, and that the on-line control is not immune from effects of cognitive aspects of the target. If this were not true, lengthening of the deceleration phase as a result of greater object fragility (i.e., object familiarity) should be quickly corrected. Recently, Gentilucci (2002; 2003b) observed that the familiarity of target objects (in this case, fruits) affects grasp parameters (maximal finger aperture), which, according to Glover, should be under on-line control. Summing up, behavioural studies suggest that on-line control is partially affected by cognitive aspects of the target. We can explain the final corrections of errors in target location, attributable to perceptual/cognitive information, by proposing that the strength of egocentric cues increases with movement progression. To this purpose, we found that fixation of the vertex of the Müller-Lyer illusion, target of a pointing movement, reduced the localization error when compared with the condition in which the other vertex was fixated (Gentilucci et al. 1997a). In other words, when the flow of information in egocentric coordinates exceeds other information, movement control is only egocentrically driven.

According to Glover, the clear-cut distinction between motor planning and on-line control finds an anatomical counterpart in two sensorimotor pathways located in the ventral and dorsal parietal-premotor cortices, respectively. An argument in favour of the hypothesis that the dorsal parietal-premotor pathway is exclusively involved in the control of movement execution is provided by motor deficits observed in patients with optical ataxia due to lesions of the posterior dorsal parietal cortex. Recently, Roy et al. (in press) studied the reaching-grasping kinematics of a patient with a unilateral lesion restricted to the posterior part of the dorsal parietal cortex. Although this patient showed an apparent recovery from optic ataxia, the early kinematic aspects of the patient's reaching-grasping movements were not normally modulated by either intrinsic or extrinsic visual properties of objects. These results constitute evidence that the posterior region of the dorsal parietal cortex, besides playing a role in the on-line control of movement execution, may also be involved in aspects of planning such as implementing and coordination of the various phases of arm movements (Gentilucci et al. 2000b; Roy et al., in press).

The ventral parietal-premotor circuit can also be involved in aspects related to perception and semantics other than those specifically related to planning an action. Indeed, neuroimaging studies have shown that the naming of tools or tool actions (Grabowski et al. 1998; Grafton et al. 1997; Martin et al. 1995), as well as viewing pictures of tools (Chao & Martin 2000), activates the human lateral premotor cortex. These findings suggest that the representations of an object (i.e., the actions associated with the object) can be automatically activated or retrieved by simply naming or viewing the object, without executing (and probably preparing) an object-related action. These results have their counterpart in behavioural data (Gentilucci 2003c) showing that class of word can be a factor selectively influencing motor control. Indeed, automatic reading of verbs more strongly influenced arm kinematics than adjectives.

Finally, action preparation and observation can be used to understand the meaning of an action (Rizzolatti et al. 2001) and to communicate with other individuals (Gentilucci 2003a; Gentilucci et al. 2001). The fact that the semantic face of speech and the arm gestures are reciprocally related, is supported by a new observation (Chieffi et al., in preparation) showing a reciprocal influence between the direction of deictic gestures (pointing towards a remote position or one's own body) and deictic terms (*QUA*, here, or *LA*', there) simultaneously pronounced. Indeed, the results showed that arm kinematics and voice spectra were reciprocally interfered with when the arm gesture was incongruent with the meaning of the deictic term.

Summing up: In our opinion, the distinction and definition of programming and on-line control of actions proposed by Glover can be partially reformulated. First, definition of on-line movement control should take into account that cognitive aspects of the object can at least partially penetrate into the feedback control of a movement. Second, definition of movement planning should take into account that some aspects of cognition (in particular semantics and speech) can be coded by action preparation.

ACKNOWLEDGMENT

This work was supported by a grant from MIUR (Ministero dell'Istruzione, dell'Università e della Ricerca) to Maurizio Gentilucci.

Plans for action

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Abstract: It is our contention that the concept of *planning* in Glover's model is too broadly defined, encompassing both action/goal selection and the programming of the constituent movements required to acquire the goal. We argue that this monolithic view of planning is untenable on neuropsychological, neurophysiological, and behavioural grounds. The evidence demands instead that a distinction be made between action planning and the specification of the initial kinematic parameters, with the former depending on processing in the ventral stream and the latter on processing in the dorsal stream.

Introduction. For the most part, Scott Glover's proposed "planning–control" model (PCM) bears a strong family resemblance to our "perception–action" model (PAM: Goodale & Milner 1992; Milner & Goodale 1995), and indeed it makes many similar predictions. But there are differences, and it is important to isolate precisely what they are, as well as to give a fair and correct account of the PAM. Take for example, this seemingly innocuous sentence taken from Glover's "Conclusions" section:

> The studies reviewed here are less consistent . . . with a perception–action model in which actions are thought to be both planned and controlled using a single visual representation in the SPL. (target article, sect. 5, para. 1)

Is this statement correct? Well, although it might be convenient for Glover if it were, the stubborn fact is that we never proposed that actions are "planned and controlled by a single visual representation in the SPL." It may suit the confrontational style of *BBS* to set up a straw man of this kind, but a closer look at what we have argued will show that the PAM makes no such simple-minded proposal. But first let us examine Glover's last clause in this sentence more closely since it does carry the germ of the real disagreement between us.

We can set to one side two relatively minor errors that are implicit in the sentence. The first error is to locate the human dorsal stream entirely within the SPL (superior parietal lobule). There is now ample fMRI evidence that the dorsal stream, particularly those regions involved in voluntary saccades and object-directed grasping, is centered on the human IPS (intraparietal sulcus), on the border between IPL and SPL (Binkofski et al. 1998; Connolly et al. 2002; Culham 2004; Culham & Kanwisher 2001; Culham et al. 2003). Only the region associated with visually guided reaching (as opposed to looking or grasping) appears to be located entirely within the SPL (Connolly et al. 2003). These neuroimaging results broadly back up the lesion localization evidence of Perenin and Vighetto (1988, Table 1), who found that a group of eight patients with optic ataxia all had brain damage that included the IPS, whereas only five of them had SPL damage. Indeed, the overlapping region in their patients was largely centered on the IPS. The

https://doi.org/10.1017/S0140525X04330025 Published online by Cambridge University Press