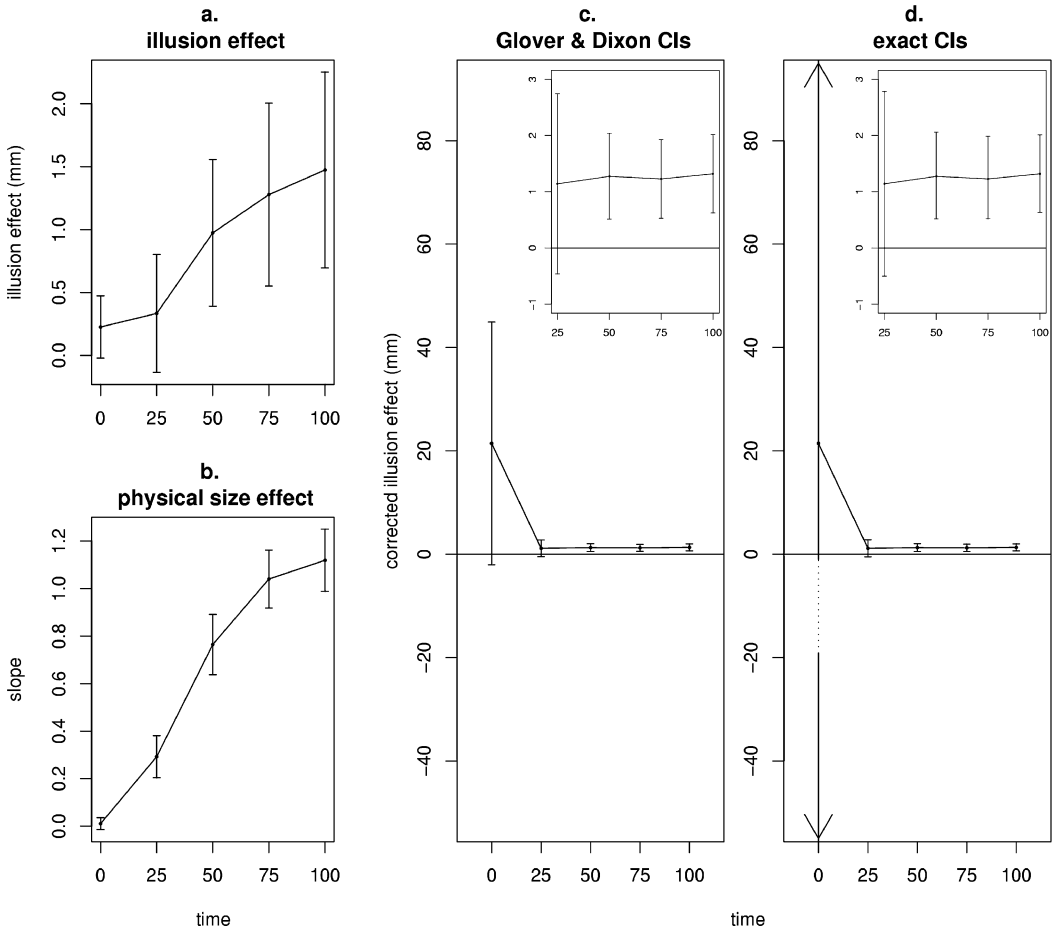


Figure 1 (Franz). Testing whether the dynamic illusion effect exists. (**1a**) Effects of the Ebbinghaus illusion on grasping as a function of time: The illusion effect is the mean difference in aperture when grasping one or the other version of the illusion. (**1b**) Effects of a physical variation of size on grasping: The physical size effect is the mean slope of the functions which relate grip aperture to physical size. (**1c**) Corrected illusion effects (i.e., illusion effects divided by physical size effects) and 95% confidence limits as calculated by Glover and Dixon's method, which ignores the variability of the physical size effects. (**1d**) Confidence limits, as calculated by the mathematically exact method (Fieller 1954; Franz, submitted): The exact method gives infinite confidence limits at $t = 0\%$; only the points on the dotted line are excluded from the confidence set, all other values are included! Data are from Franz (2003). Time is normalized, such that $t = 0\%$ corresponds to the start of the movement and $t = 100\%$ to the time of the maximum grip aperture (MGA). The insets magnify the data between t = 25% and $t = 100\%$. Error bars depict 95% confidence limits.

well beyond the time of the MGA. Most likely the fingers touched the target object at these late time points, because the trajectories were analyzed until the thumb ceased to move in a forward direction. Try it yourself: Place an object in front of you, grasp it, and move it back toward yourself (as participants did in the Glover & Dixon [2002a] study). Usually, you will have touched the object when your thumb no longer moves forward. Including time points in the analysis when participants have already touched the target object leads to a decrease of the illusion effects which is simply due to the mechanical interaction with the object and not to neuronal control processes.

In my opinion, the case of the dynamic illusion effect is not yet resolved. One possibility is that a dynamic illusion effect only shows up if participants can see their fingers during grasping. In contrast, in our studies participants could not see their fingers during grasping (note, however, that Glover and Dixon found the largest decrease in such an open loop condition). Future research should clarify this issue.

Finally, it would be interesting to know what the results of the Glover and Dixon studies would look like, if they used the mathematically exact method to calculate confidence limits and if they excluded parts of the trajectories at which participants touched the target object. Will the dynamic illusion effect survive these tests?

ACKNOWLEDGMENTS

I wish to thank Ian M. Thornton and Anne-Marie Brouwer for very helpful comments on this manuscript.

Do movement planning and control represent independent modules?

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Abstract: We address three issues that might be important in evaluating the validity of the planning–control model: (1) It could be artificial to distinguish between control and planning when control involves the re-planning of a new corrective submovement that overlaps with the initial response; (2) experiments involving illusions are not totally compelling; (3) selectively implicating the superior parietal lobe in movement control and the basal ganglia in movement planning, appears questionable.

In this interesting article, Glover reviews evidence for a dichotomy between the planning and on-line control of actions. Although we

https://doi.org/10.1017/S0140525X04320029 Published online by Cambridge University Press

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/S0140525X04320029 Published online by Cambridge University Press