

ski et al. (1998) have shown that damage to putative AIP results in impairments of visually-guided grasping.

In contrast to optic ataxia, ideomotor apraxia is a disorder that primarily affects planning of skilled actions, while leaving on-line control relatively unaffected. For example, these patients often have considerable difficulty pantomiming tool-use actions, yet have little or no difficulty reaching and grasping visually presented objects (for a comprehensive review see Heilman, 1997). Since the turn of the previous century, it has been known that ideomotor apraxia results almost exclusively from damage to, or disconnection of, the left cerebral hemisphere (Leiguarda & Marsden 2000). Recent analyses implicate both the IPL and SPL in this disorder. Lesion overlap is most frequent in areas within and adjacent to the left IPS, including SPL (BA 7) and IPL (BA 39 and 40), as well as interconnected regions of the middle frontal gyrus (GFm: Haaland et al. 2000). Corroborating evidence comes from several functional neuroimaging studies of healthy adults showing activation of these regions during overt or imagined tool use actions involving either hand (Choi et al. 2001; Johnson-Frey 2003; Moll et al. 2000). Together, these findings indicate that representations necessary for planning skilled movements involve a left-lateralized parieto-frontal system. Further, this cerebral asymmetry appears to be true regardless of one's hand dominance (Johnson-Frey et al., submitted; Lausberg et al. 1999; Raymer et al. 1999). This contrasts sharply with the apparent contralateral organization of parietal mechanisms involved in on-line control that are damaged in optic ataxia. These differences should serve as an important constraint on theories concerning the organization of action representations.

Glover is correct in asserting that the contrasting deficits of optic ataxia and ideomotor apraxia patients suggest that actions do not depend on a unitary representational system. However, the distinction is not between planning and control but, rather, between actions that are planned and controlled entirely on the basis of immediate perceptual information versus skills that additionally involve accessing stored memories (Johnson-Frey 2003; Johnson-Frey & Grafton 2003). As reviewed above, on-line manual actions are controlled by functionally specialized parieto-frontal circuits that include contralaterally organized regions belonging either to the SPL or the IPL. By contrast, in the vast majority of individuals, manual skills (e.g., tool-use) are represented in a left lateralized parieto-frontal system. Of course, the actual implementation of a skilled action in the real world necessarily involves cooperation between these two systems.

In short, this position differs from Glover's in at least two respects. First, planning takes place in *both* representational systems, but for different types of actions; that is, skills versus non-skills. Second, depending on nature of the movement(s) involved (e.g., reaching, grasping, saccades), control can be accomplished in the SPL and/or IPL.

## Is there an independent planning system? Suggestions from a developmental perspective

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**Abstract:** Glover argues that separate representations underlie the planning and the control phase of actions, and he contrasts his model with Goodale and Milner's perception/action model. Is this representation indeed an independent representation within a more general action system, or is it an epiphenomenon of the interaction between the perception/action systems of the Goodale–Milner model?

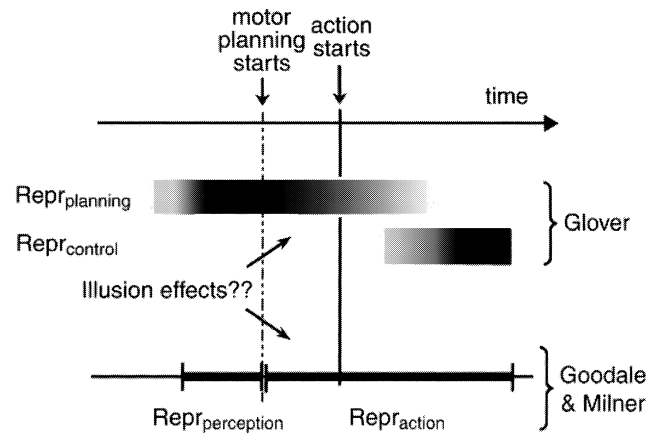


Figure 1 (Káldy & Kovács). Comparison of the Glover and the Goodale–Milner models. This schematic diagram represents the temporal relations between the two separate visual representations according to the Glover versus the Goodale–Milner model. In our view, the most significant difference is in how the two models conceptualize the acting representation between the beginning of motor planning and action.

We contrast the Glover and the Goodale–Milner models in Figure 1. According to our understanding, one of the main differences between them is the way they conceptualize the representation that the motor program is based on. In the Goodale–Milner model (Goodale & Milner 1992), it is the “action” representation of the dorsal stream ( $\text{Repr}_{\text{action}}$ ); while in Glover's model, it is a representation underlying the planning phase ( $\text{Repr}_{\text{planning}}$ ). The two models disagree about the potential effects of visual context on this representation. According to Glover's model, context has a potentially large effect on  $\text{Repr}_{\text{planning}}$ , while in the Goodale–Milner theory it does not (or the effect can only be small). Glover also claims that  $\text{Repr}_{\text{planning}}$  determines certain parameters of the motor program, such as lifting force, posture choice, movement time and grip acceleration, and these parameters can be strongly influenced by illusion effects (see Glover, sect. 2.6.1. para. 4). Not all motor program parameters are under the control of  $\text{Repr}_{\text{planning}}$ ; some – such as maximum grip aperture and pointing accuracy – are driven by  $\text{Repr}_{\text{control}}$ , and these are the parameters that context-induced illusions do not influence.

We propose an experiment motivated by our recent developmental studies that could significantly contribute to this issue. We have studied four-year-old children's and adults' performance in a 2AFC version of the Ebbinghaus illusion (Titchener circles) task (Káldy & Kovács 2003; see also Kovács 2000). Both children and adults were asked to decide which one of the target circles amidst the context circles appeared larger. The task was entirely perceptual, that is, no action was required toward the target circles. Our results have shown that the magnitude of the illusion effect was significantly smaller in children than in adults, and our interpretation is that visual context integration is not fully developed in four-year-olds. In terms of the Goodale–Milner model, we found an age-dependent effect of the magnitude of the context-induced illusion on  $\text{Repr}_{\text{perception}}$ . We proposed earlier that the ontogenetic development of the dorsal “action” system is faster than that of the ventral “perception” system in humans (Kovács 2000). Based on the age-dependent illusion effect on  $\text{Repr}_{\text{perception}}$  and on the faster maturation of the “action” system, we suggest an experiment that could decide about the independent existence of the “planning” system in Glover's model. As Glover suggests, there are particular parameters of movement that seem to be affected by illusions because they are determined by  $\text{Repr}_{\text{planning}}$ . Movement time as measured in the Ebbinghaus illusion is one of those parameters (van Donkelaar 1999). Taking into account the faster

maturation of planning related areas, the Glover model would predict that children should demonstrate adult-like illusion effects in terms of movement time well before they do in the perceptual version of the Ebbinghaus illusion task. However, the Goodale–Milner model, in the strict sense, does not allow for illusion effects arising from the “action” system; therefore, the origin of the illusion should be in  $Repr_{perception}$ . In this case, young children should behave the same way as in the perceptual task: They should demonstrate much smaller illusions than adults. This test would be an interesting way to study the relationship between the two hypothetical concepts,  $Repr_{planning}$  and  $Repr_{perception}$ , and the controversial period before the action starts.

### Action planning in humans and chimpanzees but not in monkeys

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**Abstract:** Studies with primates in sequence production tasks reveal that chimpanzees make action plans before initiating responses and making on-line adjustments to spatially exchanged stimuli, whereas such planning isn't evident in monkeys. Although planning may rely on phylogenetically newer regions in the inferior parietal lobe – along with the frontal lobes and basal ganglia – it dates back to as far as five million years ago.

Glover argues that planning is largely the province of a phylogenetically newer cortex in the inferior parietal lobe (IPL), and he suggests that “the role in the human IPL in action planning may have arisen quite recently in evolution and may be manifest in the uniquely human population lateralization in hand preference” (target article, sect. 1.2.1). Although planning is limited in macaque monkeys, as he suggests, a series of studies have revealed that chimpanzees, which are hominoids, are greatly skilled in action planning, just as humans are.

Ohshiba (1997) compared the reaction time of macaque monkeys and a chimpanzee in a sequence production task. Both species of primates were taught to select differently sized circles in an arbitrarily defined order. An analysis of the reaction times suggested that the monkeys identified only the first target to be selected in the task; and only after (and/or during) the selection of that target – which resulted in its disappearance – would they search for the next target to be selected. This was because reaction times to subsequent targets decreased in a monotonic function. In contrast, a chimpanzee doing the same task spent the longest amount of time in selecting the first item of the sequence, followed by shorter reaction times for the remaining items. These reaction times did not differ from each other. These results suggest that monkeys employ a serial search strategy, whereas chimpanzees plan before selecting the first item in a sequential task.

Kawai and Matsuzawa (2000b) provide more decisive evidence for chimpanzees' ability to plan. The chimpanzee named Ai learned to count dots on a computer monitor as well as count real objects, and to select the corresponding Arabic numerals on a touch-sensitive monitor (Matsuzawa 1985). Ai also learned to order the numbers from zero to nine in sequence, regardless of the inter-integer distance. Utilizing her numerical skills, we set up a memory task. In our experiment, three to five random but different numerals picked from 0–9 were distributed on a touch-sensitive monitor (e.g., 1, 3, 4, 6, and 9). Ai was required to select the numerals in an ascending order. Immediately after selecting the lowest numeral (i.e., “1”), all the remaining numerals were masked by a white square (Fig. 1). Therefore, Ai had to memorize the numerals (now masked) accurately to select the correct sequence. Ai attained more than 90% accuracy with four numerals and 65% with five, significantly above chance in each case (17%



Figure 1 (Kawai). The chimpanzee Ai performing the numerical ordering task in the “masking” trial (Kawai & Matsuzawa 2000b). The numerals were presented on the touch-sensitive monitor. Immediately after Ai had correctly chosen the lowest numeral (1), the remaining numerals were automatically masked. Ai continued to identify the numerals one by one in ascending order.

and 4%, respectively). In this and other similar studies (Kawai 2001; Kawai & Matsuzawa 2000a; 2000b; 2001a; 2001b), only the reaction time for the first numeral was longer than those for the remaining numerals, which did not differ (Fig. 2). These results indicate that she could memorize the correct sequence of any five numerals (Kawai & Matsuzawa 2000b).

The chimpanzee Ai also exhibits skillful on-line control of action. In the same numerical ordering task with three different numerals (e.g., 1, 3, 7), the on-screen positions of the remaining two

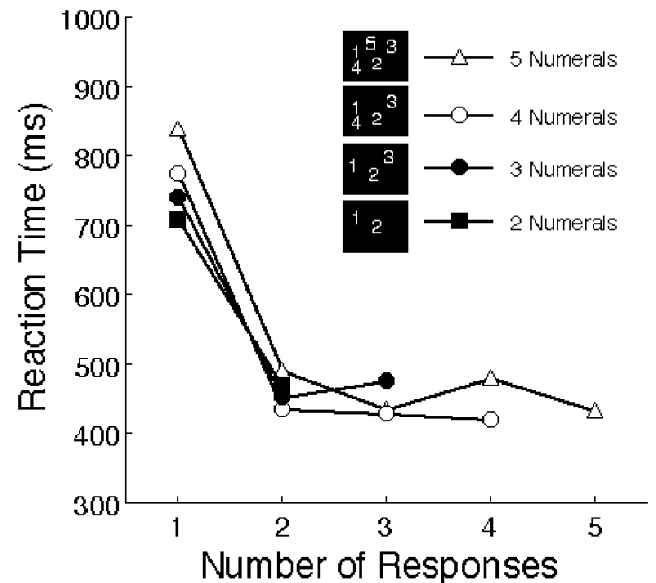


Figure 2 (Kawai). Reaction times selecting the first, second, third, fourth, and fifth items in the numerical ordering task with the chimpanzee Ai (Kawai 2001). Only the reaction time for the first numeral was longer than those for the remaining numerals, which did not differ.