

Grasping the past: delay can improve visuomotor performance

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“Optic ataxia” is caused by damage to the human posterior parietal cortex (PPC). It disrupts all components of a visually guided prehension movement, not only the transport of the hand toward an object’s location [1], but also the in-flight finger movements pretailored to the metric properties of the object [2–4]. Like previous cases [4, 5], our patient (I.G.) was quite unable to open her handgrip appropriately when directly reaching out to pick up objects of different sizes. When first tested, she failed to do this even when she had previewed the target object 5 s earlier. Yet despite this deficit in “real” grasping, we found, counterintuitively, that I.G. showed good grip scaling when “pantomiming” a grasp for an object seen earlier but no longer present. We then found that, after practice, I.G. became able to scale her handgrip when grasping a real target object that she had previewed earlier. By interposing catch trials in which a different object was covertly substituted for the original object during the delay between preview and grasp, we found that I.G. was now using memorized visual information to calibrate her real grasping movements. These results provide new evidence that “off-line” visuomotor guidance can be provided by networks independent of the PPC.

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Results

Experiment 1

In the first test session, I.G. performed three different tasks in the following order: perceptual matching, delayed

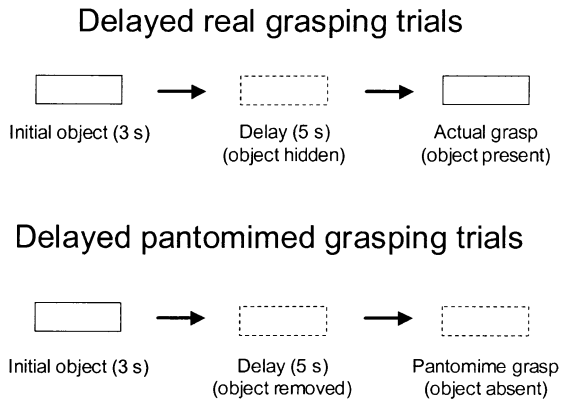
real grasping, and delayed “pantomimed” grasping. The perceptual task required the patient to make a simple manual size estimate using her forefinger and thumb. The two delayed grasping tasks were based on methods devised by Goodale and colleagues [6]. In the case of pantomimed grasping, the subject was required to delay grasping the object for 5 s, during which time the object was removed, and then to *pretend* to grasp it (see Figure 1). In the delayed “real” grasping task, the object remained present during and after the delay, so that visual information remained available “on-line” to guide the grasping action. This task was used for comparison because it more closely resembles the time course of the pantomime-grasping task than does a straightforward immediate grasping task.

The results are shown in Figure 2. We found that our optic ataxic patient I.G. reliably varied her finger-thumb grip in proportion to the object size in the perceptual task (Figure 2a), as has been reported before in such patients [5]. As predicted, she also showed reliable grip scaling in the delayed pantomime task (Figure 2c). Thus, I.G. could tailor her grip to the size of the object both in an explicitly perceptual task (matching) and in one that relied on a visual memory (pantomimed grasping). Yet much as expected, there was only weak evidence of grip scaling in the delayed real grasping task (Figure 2b). I.G.’s grip aperture was variable from trial to trial, in contrast with the high consistency of her perceptual estimates and pantomimed grasps.

These data demonstrate a paradoxical improvement of grip scaling when the stimulus was no longer present, the opposite of what would be expected in normal subjects [6]. Nevertheless, there was still a mild trend for grip scaling in the delayed real grasping task, a trend that had not been predicted. We therefore tested I.G. in a second session in which we compared delayed real grasping with standard immediate grasping.

In this second session, I.G. performed the following tasks: immediate grasping, delayed real grasping, and delayed pantomimed grasping. The three tasks were presented according to an “abcba” design. As predicted, we found no significant grip scaling during immediate grasping (Figure 3a), as in previously reported patients [4, 5]. In delayed real grasping, however, grip scaling was now very clearly observed, with I.G. opening her hand significantly less widely for the narrowest object in comparison with the other three objects (Figure 3b). Finally, as predicted, clear grip scaling was again found in the delayed pantomime-

Figure 1



The delayed grasping tasks used in the present study. In both delayed tasks (real and pantomimed), the object was first viewed for 3 s, and then shielded from view for 5 s. In delayed real grasping, the subject then had to reach out and grasp the object. In pantomimed grasping, however, the subject had to *pretend* to reach out and grasp the object after this delay, as it had been covertly removed during the delay period.

grasping task (Figure 3c). There was also a notable general reduction in I.G.'s initially exaggerated grip apertures from the first to the second testing blocks.

Thus, I.G. was unable to scale her grip size when a simple immediate grasp was required; yet, having previewed the object 5 s before being offered it to grasp, she now adjusted her grip aperture quite well. Of course, in contrast to the immediate or pantomimed tasks, for which only one source of visual information could be used, both present and past visual information is potentially available in

the delayed real grasping task. We had initially assumed, however, that the past information would be entirely superseded by the new sensory information available to the visuomotor system, as was shown in a different context for proprioceptive targets [7].

But in I.G.'s case, that past information would *not* be redundant. Indeed, her relative success in pantomimed grasping shows that it would now provide her with better visual guidance than the current information, processed within her damaged visuomotor system. It is therefore possible that I.G. might have adopted a pantomiming strategy in the delayed real grasping task, rather than relying on the currently visible object to guide her hand. Support for this superficially implausible idea comes from I.G.'s reduced grip aperture during the second block of delayed real grasping trials; previous work has shown that people open the hand less widely when *pretending* to reach out and grasp than when actually doing so [6].

In order to determine which of the two sources of visual information was used during delayed real grasping by I.G. and by healthy subjects, we created a new series of delayed real grasping trials in which occasional special test trials were embedded. The task was given after a series of standard delayed real grasping trials and was presented as yet more of the same task.

Experiment 2

In this experiment, only delayed real grasping was tested. However, although the usual four objects were used throughout, half of the trials with the widest and narrowest objects were made into test trials. On these occasions, the narrowest (2 cm) object was covertly replaced during the

Figure 2

Experiment 1: I.G.'s maximum grip aperture (MGA) during a perceptual matching task and two delayed prehension tasks. Within each block of trials, each object was presented four times in a pseudo-randomized order (no object was presented twice in succession). Linear regression analysis showed that I.G. scaled her grip size in relation to object width at high levels of significance in both (a) the matching task ($r^2 = 0.80$; $F[1,14] = 56.08$, $p < 0.001$) and (c) the delayed pantomime task ($r^2 = 0.66$; $F[1,14] = 26.75$, $p < 0.001$). There was much less indication of grip scaling in the (b) delayed real grasping task, though it did just reach significance ($r^2 = 0.26$; $F[1,14] = 4.97$, $p < 0.05$). Grip size varied from trial to trial considerably more during delayed real grasping (average SD per object width = 13.65) than during pantomimed grasping (average SD = 6.48) or perceptual matching (average SD = 4.38).

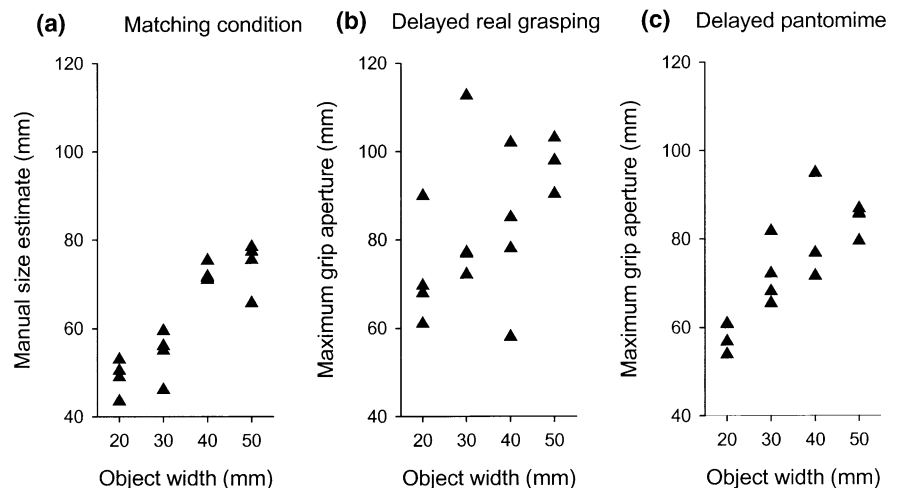
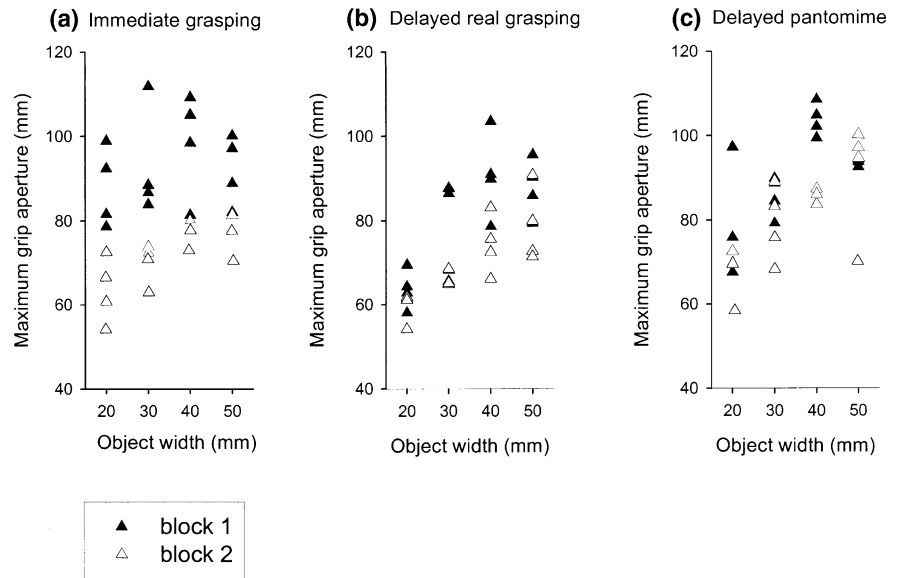


Figure 3

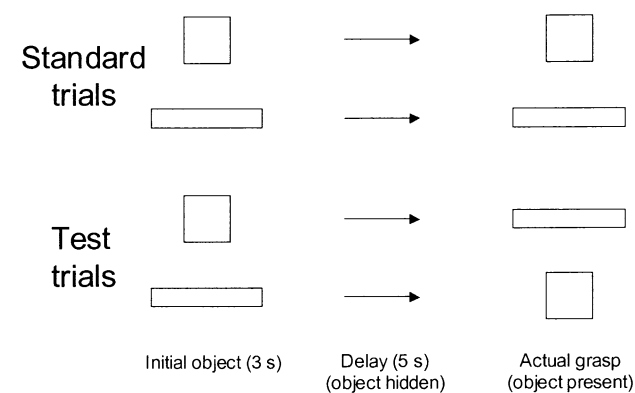
Experiment 1: I.G.'s maximum grip aperture during three different prehension tasks. **(a)** In the immediate grasping task, the subject simply had to reach out to pick up the target object, front to back using forefinger and thumb, as soon as it became visible. Linear regression showed no significant relationship between object width and MGA during this task ($r^2 = 0.08$; $F[1,30] = 2.53$). **(b)** During delayed real grasping, however, clearly significant grip scaling was observed ($r^2 = 0.43$, $F[1,30] = 22.91$, $p < 0.001$). **(c)** As expected, highly significant grip scaling was also found in the delayed pantomime grasping task ($r^2 = 0.40$, $F[1,30] = 19.83$, $p < 0.001$). In all three tasks, MGA was significantly smaller during the second block of trials (immediate grasping: $F[1,24] = 46.37$, $p < 0.001$; delayed real grasping: $F[1,24] = 20.82$, $p < 0.001$; delayed pantomimed grasping $F[1,24] = 11.74$, $p < 0.005$).



delay interval with the widest (5 cm), or the widest was replaced with the narrowest (see Figure 4). In total, 48 trials were performed in a pseudo-randomized order (12 for each object, including 6 “test” trials for the widest and 6 for the narrowest object). Six age-matched right-handed healthy control subjects were also tested using the same paradigm.

We confirmed that our controls opened their hands during the prehension movement entirely according to the size of

Figure 4



A schematic depiction of Experiment 2. In a quarter of all trials, the widest object (50 mm) was covertly replaced by the narrowest (20 mm), or vice-versa, during the delay period (bottom). In another quarter of the trials, the narrowest and widest objects remained unchanged (top). In the remaining half of the trials, objects of intermediate widths were used (30 and 40 mm, not depicted here) and remained unchanged throughout each trial.

the object facing them (Figure 5b). It made no difference whether or not they had been shown a different block 5 s earlier. In striking contrast, I.G. opened her hand widely when the wide object had been previewed, even when reaching out to grasp the narrow one (Figure 5a, right). Evidently I.G. used a memory-based route to bypass her visuomotor deficit, while the controls never did this.

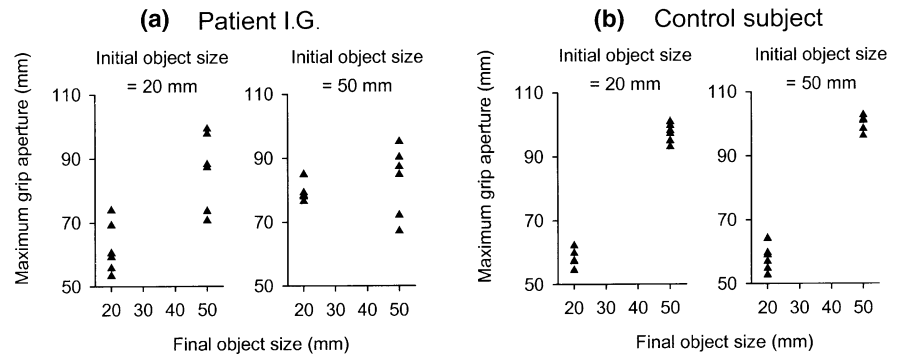
In the test trials in which the narrow object was replaced by the wide one, I.G.'s maximum grip did reach an appropriately wide aperture (Figure 5a, left). Presumably, the initially programmed small grip aperture had to increase during the course of the reach in order for I.G. to eventually grasp the wide object, and this would be reflected in the maximum grip aperture that we measured. Of course, on the trials when she had to close down her grip from an expected large to an actual small object, that small object was also eventually grasped correctly, but the grip would already have opened widely before that correction occurred.

Discussion and conclusions

Patient I.G. suffered severe bilateral damage to the homolog of the monkey's “dorsal stream” of visual processing, causing the visuomotor difficulties typical of optic ataxia. The primate dorsal stream plays a specialized role in the on-line automatic transformation of visual information into action coordinates [8–13], and indeed lesions there result in deficits closely resembling human optic ataxia [14, 15]. This pattern contrasts strikingly with the effects of damage to the primate ventral stream, which cause profound problems in shape discrimination but spare visually controlled reaching and grasping [16, 17]. In a similar

Figure 5

Experiment 2: maximum grip aperture as a function of final object size for patient I.G. and one representative control subject. The MGA data were analyzed for each subject individually using ANOVAs with initial and final object size as independent variables. For all of the subjects, there was a significant main effect of final object size ($p < 0.005$), but none of initial object size. However, there was a significant interaction between initial and final object size for patient I.G. only ($F[1,19] = 7.01$, $p < 0.02$). Inspection of the data reveals that, when the initial object was 5 cm wide and covertly replaced by the 2-cm wide object, I.G. programmed her grip size on the basis of the initial large object width. All of the six control subjects always used the final object size for programming their MGA, irrespective of whether it had changed during the trial.



way, the well-tested patient D.F., whose visual-form agnosia renders her unable to distinguish simple shapes or contours, can nevertheless perform a range of actions guided by those same visual features [18, 19]. D.F.'s lesion has bilaterally disconnected her ventral stream from most of its visual inputs [20].

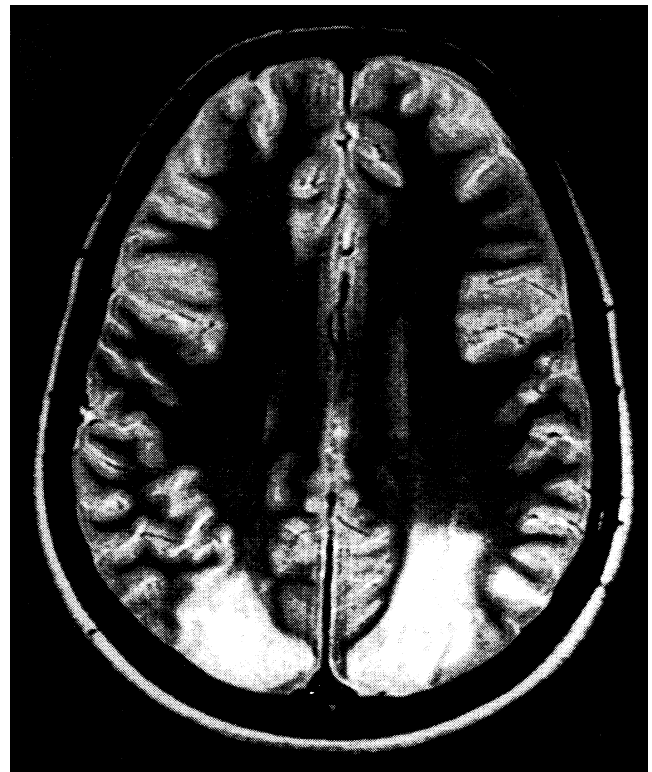
This double dissociation provided the rationale for the present study. The intact visuomotor skills retained both by "agnosic" monkeys and by the agnosic patient D.F. have been attributed to an (largely) intact dorsal stream [21]. Yet, Goodale and colleagues [6] found that D.F. was unable to respond appropriately when asked to perform pantomimed grasps in response to a memorized object no longer present. They proposed that healthy observers perform such delayed acts by means of a conscious perceptual representation of the object, rather than through direct visuomotor control. This indirect route would not be available to D.F., because she cannot achieve the necessary perceptual representation.

This proposal of two separate routes from vision to action [6] is attractive, but it relied entirely on *negative* evidence, in that patient D.F. performed exceptionally badly on the delayed task. We therefore sought complementary positive evidence from optic ataxia, making the prediction that patient I.G. should show improved performance in delayed pantomime grasping relative to immediate grasping, a converse pattern to that seen in healthy subjects. We assumed that I.G. might be able to circumvent her damaged visuomotor system by bringing her relatively intact perceptual system into play.

In Experiment 1, we established that I.G.'s visuomotor difficulties included the misgrasping of objects of different widths presented to her in her peripheral vision. At

the same time, we showed that, like previous patients [5], I.G. perceived the object widths quite accurately and could signal these percepts using her finger and thumb. Most crucially, we confirmed our prediction that she should show an improvement in her grasping movements

Figure 6



A coronal section through I.G.'s brain, visualized with structural MRI. Extensive damage is present bilaterally in the posterior parietal lobes.

when performing a pantomime task; I.G. now showed good grip scaling. These findings thus provide the other half of a double dissociation along with the data from D.F. [6]. They are clearly consistent with the idea that posterior parietal visuomotor systems are part of the neural circuitry for mediating normal immediate object grasping [11, 13] but are not essential for mediating *delayed* responses of an ostensibly similar kind [7, 22].

We correctly predicted good pantomimed grasping by I.G.. However, we expected that her *real* grasping behavior would be equally impaired whether or not she had seen the object a few seconds earlier. We wrongly assumed that I.G. would try to use the same visual information in both cases, namely, the information present in her visual field at the moment of reaching out for the object. In Experiment 2, we showed that she achieved her surprisingly good delayed real grasping through a strategy quite different from that used by normal observers. We showed this by interspersing “invalid” probe trials within a delayed real grasping session. Healthy control subjects invariably ignored the previewed information. In sharp contrast, I.G. evidently depended on this previewed information, programming her grasp without regard to the current visual information. Consequently, when a wide object was, unbeknown to her, replaced by a narrow one, she opened her handgrip too widely for the object in front of her.

The present data support the idea that vision can guide action through networks other than the dedicated systems of the parietal lobe. These networks have different time constraints and different cognitive loadings attached to them [7, 23, 24]. Use of such alternative networks evidently allowed I.G.’s grasping difficulties to be circumvented, albeit by taking a slow and circuitous route from vision to action.

Materials and methods

Patient

I.G. had suffered a bilateral parieto-occipital infarction 17 months before the present testing (see Figure 6). She initially presented with severe headache and dysarthria and bilateral blindness lasting for 3 days. Following this, bilateral optic ataxia and simultanagnosia became apparent [11, 25]. The patient had a diagnosis of ischemic stroke, related to acute vasospastic angiopathy in the posterior cerebral arteries. MRI revealed a hyperintense signal on T2 sequences that was near-symmetrically located in the posterior parietal and upper and lateral occipital cortico-subcortical regions. Reconstruction of the lesion indicated that it mainly involved Brodmann’s areas 7, 18, 19, the intraparietal sulcus, and part of area 39. I.G. was aged 31 when we tested her, by which time her simultanagnosia had subsided, at least for presentations of two to three objects [11].

Apparatus

As in several previous studies [6, 19], we used rectangular blocks varying in width, but of constant surface area. Four different blocks were used, with the dimensions: 5 cm × 5 cm, 4 cm × 6.25 cm, 3 cm × 8.3 cm, and 2 cm × 12.5 cm. They were made of dark gray plastic with a thickness of 1 cm and were presented on a table against a white background. Due to the fact that I.G.’s optic ataxia chiefly affects nonfoveal vision, we

presented the objects eccentrically, using a central red fixation spot. The left edge of each object was positioned 6 cm (approximately 5°) to the right of this spot. Fixation was checked continually by an experimenter facing the patient.

Grip aperture was measured by means of a magnetic movement recording system (Minibird, Ascension Technology), with markers attached to the tips of the forefinger and thumb. This allowed us to record finger-thumb separation, in 3D space, throughout all of the reaching and grasping movements, or for 1 s in the case of I.G.’s size judgements in the perceptual matching task. The dependent variable of interest was the maximum grip aperture attained during reaching (MGA), or the mean finger-thumb aperture in the case of perceptual matching. These measures are linearly related to object size in healthy subjects in all of the tasks. In grasping tasks, MGA provides a direct index of the use of visual information in advance of contact with the object [26].

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