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DIFFERENCES IN THE VISUAL CONTROL OF PANTOMIMED AND NATURAL GRASPING MOVEMENTS

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Abstract—In a series of experiments, we studied the differences between natural target-directed grasping movements and 'pantomimed' movements directed towards remembered objects. Although subjects continued to scale their hand opening for object size when pantomiming, grip formation and other kinematic variables differed significantly from those seen in normal target-directed actions. This was true whether the subjects had just seen the target object 2 sec before (Experiments 1 and 2) or whether the target object was still present and they were simply required to pantomime the grasping movement beside it (Experiment 3). We argued that these pantomimed reaches were being driven by stored perceptual information about the object, and were not utilizing the normal visuomotor control systems that direct actions in real time. This interpretation received strong support from observations of a patient with visual form agnosia who was also tested. In an earlier report, we had shown that this patient showed anticipatory scaling of her grasp despite her inability to discriminate between objects perceptually on the basis of size. The present study showed, however, that the requirement to remember an object even briefly, or to pantomime an action beside it, was enough to completely disrupt her visuomotor scaling (Experiments 2 and 3). That this reflected a failure of perception rather than imagery or understanding was supported by the fact that she could convincingly pantomime actions to imagined, familar objects, the sizes of which were known to her (Experiment 4). All these results suggest that the mechanisms underlying the formation of perceptual representations of objects are quite independent of those mediating on-line visuomotor control.

INTRODUCTION

When confronted with a goal object, particularly an unfamiliar one, the visuomotor systems mediating manual prehension must compute the size, shape, orientation, and position of the object and transform that information into a coordinated grasp. Without such computations, the hand could not be directed to the location of the object, nor could the posture of the fingers be adjusted in anticipation of the final grasp (for a discussion of these issues, see [11, 16]). Moreover, the temporal constraints on the control of prehension, particularly on the amendments made during the execution of the constituent movements, demand that the underlying computations be both fast and robust. In addition, because the required actions must be matched to the location and disposition of the object with respect to the observer, these computations must be organized within viewer-centred frames of reference.

But observers and objects often move relative to one another, and thus the egocentric coordinates of the goal object can change considerably from moment to moment. This is true not only for the location of the object in egocentric space, but also for the orientation of the

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object in that space. Thus, the affordances offered for grasping the object could change drastically as the size, shape, and orientation of the object surface facing the observer changed. As a consequence, it would be efficient to compute the required coordinates for action immediately before the movements are initiated and it would be quite inefficient to store such coordinates (or the resulting motor programs) for more than a few milliseconds before executing the action. For this reason, the introduction of even a small delay between viewing the goal object and initiating a grasping movement might be expected to result in a marked change in the organization of the constituent movements. In short, movements directed to remembered objects should be different from movements directed to objects in 'real time'.

Such effects have been observed in studies of saccadic eye movements. Saccades made 1–3 sec following the offset of a target light were found to be 10–15 msec longer and to achieve lower peak velocities than saccades directed toward an identical target that remained illuminated [1]. In addition, the coupling between peak velocity and movement amplitude is much more variable in saccades made to remembered rather than visible targets [24]. Memory-driven saccades are also less accurate than those made to visible targets [7]. Indeed, an increase in the incidence of terminal errors has been seen even when the delay between target offset and the initiation of the saccade is as short as 100 msec. Moreover the amplitude of these errors increased as the delay was lengthened systematically up to delays of 2 sec. This latter observation led Gnadt *et al.* [7] to propose that in the oculomotor system a transition between visually-linked and memory-linked representations occurs during the first 800–1000 msec following offset of a visual target and that "the 'memory' of intended eye movement targets does not retain accurate retinotopic registration" (p. 710). In summary, these differences in saccadic dynamics and accuracy suggest that the coordinates and neural subsystems generating saccades to remembered locations are to some degree independent from those subserving normal target-driven saccades (see, e.g. Refs [12, 13]).

Similar differences between target-driven and memory-driven movements might also be expected in manual prehension. To examine this possibility, in the first experiment described below, we compared the kinematics of normal grasping movements with the kinematics of movements made by subjects when they were required to initiate such movements 2 sec after having last viewed the target object. In essence, subjects were required to 'pantomime' the grasping movement in the delay condition since the object was no longer present when the movement was initiated. We also examined the effects of blocking or randomizing the order of trials requiring memory-driven (pantomimed) and target-driven (normal) movements. This was done to examine whether or not the subjects' expectancies regarding task requirements would influence their movement planning and execution. It was predicted that, while hand shaping during pantomimed actions would continue to reflect the subjects' 'knowledge' of the characteristics of the target objects just seen, detailed kinematics of pantomimed actions would be very different from those of goal-directed actions—just as memory-driven saccades differ from target-initiated saccades.

EXPERIMENT 1

Method

Subjects. The subjects were 12 right-handed females ranging in age from 20 to 29 years (mean age 22.4 years). All subjects were students at the University of Western Ontario and all were paid for their participation.

Apparatus. Movement kinematics were recorded with a WATSMART optoelectronic recording system (Northern Digital Inc., Waterloo, Canada). In the experiments reported in this paper, three infrared-light emitting diodes (IREDs), approx. 4 mm in diameter, were attached to the dorsal surface of the right hand. One IRED was placed on the left edge of the nail of the index finger, another on the right edge of the thumbnail, and a third on the left side of the wrist opposite the styloid process. The positions of these IREDs were sampled at 100 Hz during each trial, and records of each movement were reconstructed in three dimensions and filtered off-line. Data analysis techniques and the accuracy of this system have been documented elsewhere [14].

On a given trial, subjects were required to pick up a red object placed in front of them on a grey table-top measuring 1.00 × 0.55 m. Three different objects were used, all matched for area on the top surface but differing in their dimensions. Specifically, the objects were a square (5 × 5 cm), a medium rectangle (3.5 × 7.15 cm), and an elongated rectangle (2.5 × 10 cm), all 1 cm in height.

A pair of adapted swim-goggles were employed in this experiment to control stimulus presentation. The plastic lenses in the goggles were replaced with liquid crystal shutters (Polytronix, Richardsom TX) which could be made 'transparent' by passing a small current through each shutter (transmission of room light is greater than 80% in this state). In their 'opaque' configuration, the subjects' visual world was a flat grey and objects on the table surface could not be seen. According to the manufacturer's specifications, the change from the opaque to the transparent configuration was 90% complete within 1 msec, while the change in the opposite direction was 90% complete within 2 msec.

Procedure. Subjects were tested in three experimental conditions (described below) the order of which was counterbalanced across subjects. Three practice trials preceded each condition.

Subjects began each trial with the right thumb and index finger touching one another and depressing a start key directly in front of them on the table surface. With the subject's goggles in the opaque configuration, the experimenter placed one of the three test objects on the table surface with its center at a distance of 20, 30 or 40 cm directly in front of the start key. After a ready signal from the experimenter, a small current was passed through the goggles via a remote switch, making them transparent. At this point, the subject simply viewed the target object for a 5 sec period, until the goggles once again became opaque. After a 2 sec interval, in which the subject could not see the table surface or the test object, the goggles were once again made transparent and, at the same time, an auditory signal indicated to the subject that she should initiate a reaching movement. Data collection began when the tone sounded, and was automatically terminated 2 sec later.

In one block of trials, the test object remained on the table surface but could not be seen during the 2 sec interval following its initial presentation. In this condition, the subject was required to reach out with her right hand and pick up the test object (using the thumb and index finger) when it came back into view at the sound of the tone. In another block of trials, the test object was always removed from the table surface during the 2 sec interval following its initial presentation. In this condition, each subject was to try to remember what the target object had looked like and where it had been located. When the tone sounded and the goggles were made transparent, the subject was to reach out and pretend to pick up the particular object she had seen during the viewing period, *as if it were still physically present.* In this condition, then, the 2 sec interval following target presentation really constituted a short retention interval. In both of these conditions, each of the three objects was presented at each of the three locations four times, for a total of 36 trials. The particular object used and its distance from the hand's start position were varied across trials in a pseudorandom order, with the stipulation that no more than three consecutive trials could be directed to the same object or location.

In a third condition, trials in which the object remained on the table surface (and was picked up) or was removed from the table surface (necessitating a pantomimed response) were presented in a pseudorandom order. During every trial, the experimenter approached and touched the table surface during the 2 sec no-vision interval so that auditory cues could not be used by the subject to discriminate between the two types of trials. There were a total of 72 trials in this condition, 36 in which the object remained present and 36 in which it was removed from the table surface. Specifically, each object was presented four times at each location in each viewing condition. No more than three consecutive trials could be to the same object or location, or in the same viewing condition.

Dependent measures. A number of dependent measures were extracted from the kinematic record of each trial. Movement onset time was determined by scanning each file to find the point at which the mean resultant velocity of the wrist IRED exceeded a value of 5.0 cm/sec over three consecutive frames. The end of the reaching (or 'pre-manipulatory') phase of the movement was defined as that point in time at which the velocity of the wrist IRED first fell below 5 cm sec. Movement duration was calculated simply by subtracting the time of movement onset from the time of movement completion.

Measurements were made of the peak resultant velocity of the wrist maximum trajectory height, maximum grip aperture, and the time at which these maxima were achieved during each reach. The distance of the wrist from the start key at the end of each movement was also noted.

For each condition, means were calculated for each dependent measure from the four repetitions with each object at each distance. In a very small proportion of trials (approx. 1%) data were lost due to technical difficulties. Only trials in which complete data were available for all dependent measures were included in the data set. In no case was any mean based on fewer than three trials.

Results

The means for each dependent measure were analyzed in a series of 2 (Order: blocked vs random) × 2 (Reach Type: normal grasp vs pantomime) × 3 (Object Width: 2.5 cm, 3.5 cm, 5 cm) × 3 (Object Distance: 20 cm, 30 cm, 40 cm) univariate ANOVAs, with repeated

Table 1. Effects of varying test condition on a variety of kinematic measures in Experiment 1 ($n=12$). Scores are summed over the 3 object distances and 3 object sizes. S.E. of mean values in parentheses

	Normal grasp	2 sec delay	F statistic
Peak velocity (cm/sec)	78.9 (1.24)	74.5 (1.21)	$F(1, 11)=7.89$, $P<0.05$
Max. aperture (mm)	92.6 (0.86)	83.0 (0.62)	$F(1, 11)=15.64$, $P<0.005$
% Time to max. aperture	70.2 (0.82)	68.2 (0.83)	$F(1, 11)=8.09$, $P<0.05$
Wrist displacement (mm)	184 (5.3)	174 (5.7)	$F(1, 11)=8.41$, $P<0.05$

measures on all factors. Geisser–Greenhouse adjustments were made to the degrees of freedom [18]. Simple contrasts were performed using the Newman–Keuls testing procedure; complex contrasts were evaluated with the Scheffé testing procedure. An alpha level of 0.05 was adopted for all tests of significance.

Pantomimed reaches differed from normal grasping responses in a number of respects, regardless of whether the trials were presented in blocked or random order. These differences are summarized in Table 1, which provides means, test statistics, and significant pair-wise contrasts. As can be seen in the table, pantomimed movements reached a lower peak resultant velocity than normal reaches. In addition, while subjects continued to scale the maximum opening of their hands for object size, maximum grip aperture during pantomimed reaches was significantly smaller than that seen during normal reaches. This was true for all target objects and target locations, although the effect was greater for the large object than for the smallest of the three objects [Reach Type × Object Width: $F(1.36, 14.97)=9.8$, $P<0.005$]. Moreover, as Table 1 shows, subjects spent proportionately less time opening their hands (and proportionately more time closing them) when their reaches were pantomimed than under normal conditions. The wrist was raised higher off the table surface during pantomimed reaches; this effect, however, was only statistically significant for objects presented at the 40 cm distance [Reach Type × Object Distance: $F(1.41, 15.47)=6.77$, $P<0.05$]. Moreover, there was a trend ($P<0.10$, n.s.) for pantomimed reaches to take longer to complete than normal reaches. Finally, movement amplitude (wrist displacement) was smaller for pantomimed actions than for normal reaches at all three target locations, although this effect was particularly striking for the closest targets [Reach Type × Object Distance: $F(1.57, 17.23)=8.96$, $P<0.005$]. In fact, this difference in movement amplitude could account in part for the difference in peak velocity between pantomimed and normal reaches described earlier.

Only two variables were affected by the order (Blocked or Random) in which the trials were run. Specifically, both wrist displacement [$F(1, 11)=9.72$, $P<0.01$] and maximum trajectory height [$F(1, 11)=6.46$, $P<0.05$] were slightly greater (3–4 mm) in the random series than in blocked presentation, on average.

The manipulations of object width and distance also affected movement kinematics (see Table 2 for means, test statistics, and significant contrasts). These effects were entirely consistent with the results of previous work in our laboratory on normal target-directed grasping movements [14]. Specifically: (1) increases in *object width* were associated with increases in maximum grip aperture and wrist displacement (with a trend for an increase in

Table 2. Effects of varying object width and distance on a variety of kinematic measures in Experiment 1 ($n=12$). Scores are summed over normal and delayed grasping movements. S.E. of mean values in parentheses. Contrasts were evaluated at the 0.05 level of significance

Object width	2.5 cm	3.5 cm	5.0 cm	Contrasts	F statistic
Peak velocity (cm/sec)	76.0 (1.51)	76.6 (1.53)	77.3 (1.49)	Not performed	n.s. $P=0.05$
Max. aperture (mm)	79 (0.7)	88 (0.8)	97 (0.9)	$2.5<3.5<5$	$F(1.40, 15.37)=341$, $P<0.001$
Wrist displacement (mm)	174 (6.7)	179 (6.8)	183 (6.7)	$2.5<3.5<5$	$F(1.18, 12.96)=26$, $P<0.001$
Object distance	**20 cm**	**30 cm**	**40 cm**	**Contrasts**	**F statistic**
Peak velocity (cm/sec)	58.1 (0.73)	78.4 (0.88)	93.6 (1.05)	$20<30<40$	$F(1.22, 13.41)=337$, $P<0.001$
Time to peak velocity (msec)	332 (4.6)	363 (5.4)	392 (5.5)	$20<30<40$	$F(1.61, 17.74)=53$, $P<0.001$
Max. aperture (mm)	87 (1.0)	88 (1.0)	89 (1.0)	$20<30=40$	$F(1.82, 20.06)=10$, $P<0.005$
Time to max. aperture (msec)	512 (8.1)	577 (10.1)	642 (11.4)	$20<30<40$	$F(1.62, 17.80)=98$, $P<0.001$
Max. wrist height (mm)	86 (1.3)	107 (1.7)	128 (2.2)	$20<30<40$	$F(1.16, 12.77)=108$, $P<0.001$
Time to max. wrist height (msec)	385 (4.5)	403 (4.4)	435 (6.5)	$20=30<40$	$F(1.31, 14.38)=14$, $P<0.005$
Wrist displacement (mm)	83 (1.7)	179 (1.5)	274 (1.7)	$20<30<40$	$F(1.77, 19.42)=8290$, $P<0.001$
Duration (msec)	718 (6.1)	834 (8.1)	971 (10.3)	$20<30<40$	$F(1.17, 12.84)=282$, $P<0.001$
% Time to max. wrist height	48.2 (0.60)	49.9 (0.57)	49.6 (0.61)	$20<30=40$	$F(1.50, 16.48)=5.77$, $P<0.05$

peak resultant velocity, $P=0.05$); and (2) increases in *object distance* were associated with increases in peak resultant velocity, maximum grip aperture, maximum wrist height and the times at which each of these maxima was attained, and with increases in movement amplitude and duration. Finally, subjects in the present study spent proportionately less time raising their limb for objects at the 20 cm distance than they did for objects which were located further away.

Discussion

As expected, subjects performed pantomimed actions in a manner quite distinctly different from the way in which they executed natural, target-directed grasping movements, and this was true whether or not they knew ahead of time that they would be required to pantomime on a given trial. Thus, mimed actions consistently reached lower peak velocities, tended to last longer, followed more curvilinear trajectories, and undershot target location, compared to normal reaches. Moreover, subjects consistently opened their hands less when miming than when reaching for objects which were physically present. Despite this, if subjects were unexpectedly given a second chance to view the target object at the end of the 2 sec no-vision interval, they reached out with no hesitation and grasped the object quite normally. Indeed, there was virtually no difference between their actions during these trials and during the block of trials in which they knew the object would be continuously present. This result suggests that visuomotor coordinates are normally computed *de novo* immediately before each action occurs. The fact that there was no difference in the movement onset times for target-directed reaches in the blocked and random conditions is also consistent with this argument. Moreover, the fact that onset times for pantomimed reaches also did not differ across these conditions suggests that they, too, were programmed *de novo* as soon as the tone was sounded. In this use, of course, the programming of the pantomimed action would have had to rely, not on current visual information, but rather on a stored representation of the object and its spatial location.

But what is the nature of this representation? If, as we have argued above, visuomotor systems operate only in real time, the stored information driving pantomimed actions must depend on another system, one designed specifically for representing objects in their spatial locations over longer periods of time—in short, on the 'perceptual' system presumed to mediate object recognition. In a recent series of articles, Goodale and Milner [8, 9, 20] have argued that it is this latter system that allows us to make conscious, perceptual judgements about objects and accumulate knowledge about them. Certainly, there is evidence in the literature on the control of saccadic eye movements to suggest that memory-driven saccades are programmed in 'perceptual' rather than egocentric (retina-based) coordinates and that the visuomotor transformations mediating those saccades may use the same visual information as the underlying perceptual reports of spatial location [25].

To test the idea that pantomimed actions depend not on stored visuomotor coordinates but rather on stored visual percepts of objects, we went on to compare the kinematic profiles of target-directed and pantomimed grasping movements made by a patient (D.F.) who has a profound deficit in object recognition (a so-called 'visual form agnosia'). Earlier work had shown that D.F. could generate well-scaled grasping movements toward objects of different sizes placed in front of her—*despite the fact that she was unable to discriminate between these objects in a variety of perceptual tests* [10]. If, as argued above, pantomimed actions depend upon stored percepts of target objects, then D.F. should be unable to pantomime grasping movements in a convincing manner. Indeed, these actions (unlike her normal target-directed responses) should betray the fact that she has no conscious 'knowledge' of the sizes of the objects that were removed from view, since she did not 'perceive' them in the first place!

In addition to testing the patient D.F., we once again examined the performance of a group of neurologically-intact control subjects on the pantomime task. This time, however, we included (in addition to the 2 sec delay) a much longer 30 sec delay, anticipating that this increase in the retention interval would make little difference to the pantomime performance of normal subjects. This prediction follows directly from the argument made above that pantomimed actions depend on the perceptual system underlying object recognition—a system which is specifically designed to maintain information over long periods of time.

EXPERIMENT 2

Method

Neurologically-intact subjects. Neurologically-intact subjects included 10 right-handed female volunteers. The mean age of this group was 25.6 years (range 20–36 years). All were students at the University of Western Ontario who were paid for their participation.

Patient D.F. The patient's history has been described in detail elsewhere [10, 21]. These reports document the presence of a profound visual form agnosia which has persisted since an accidental carbon monoxide poisoning in 1988. They also demonstrate, however, that D.F.'s visual fields remain essentially normal out to 30° and that the

P100 to a flashed checkerboard is consistently prominent and bilaterally symmetrical (suggesting that visual information is reaching at least primary visual cortex, which also appears intact on MRI). Although contrast sensitivity is impaired by 1 log unit at spatial frequencies of 5 cpd and lower, at higher spatial frequencies she shows normal contrast sensitivity functions. Additional sensory testing revealed that her performance in the luminance domain is somewhat compromised, but her color vision remains relatively intact. In any case, the pattern of her sensory deficits cannot account for her profound difficulty with form and pattern dicriminations; many individuals with far worse sensory deficits arising from peripheral damage to the visual pathways have little difficulty on discrimination problems that for D.F. are insurmountable.

The present experiment was carried out 3 years after D.F.'s accident, when the patient was 37 years of age.* D.F. performed the experimental task using her dominant, right hand. Although D.F. does experience some memory problems, during the present testing session we verified that her digit span was normal in that she had no difficulty remembering the position of a target object amongst eight identical distractors even for delays of up to 30 sec (the longest retention interval tested).

Apparatus. The apparatus was identical to that described in Experiment 1, except that the liquid crystal goggles were not used to control stimulus presentation. Objects of the same dimensions as those used in Experiment 1 were employed, but for the present study the objects were painted white rather than red, and were presented on a black background. Once again, the objects were a square (5 × 5 cm), a medium rectangle (3.5 × 7.15 cm), and an elongated rectangle (2.5 × 10 cm), all 1 cm in height. These objects are a subset of those used in our original studies of D.F. [10]. We have shown, using a variety of experimental procedures, that D.F. consistently fails to discriminate between these objects at a 'conscious', perceptual level. (This perceptual failure is documented in Experiment 4, below.)

Procedure. In preparation for a given trial, each subject sat with her eyes closed and with the tips of her right thumb and index finger touching one another and depressing the 'start' key. While the subject's eyes were closed, the experimenter placed one of the three test objects on the table surface, with its center at a distance of 20, 30 or 40 cm directly in front of the start key. On a verbal command from the experimenter, the subject opened her eyes and viewed the target object for a period of 5 sec, after which the experimenter gave a verbal command for her to close her eyes. At this point the subject waited for an auditory signal to reopen her eyes and initiate her reaching movement (see below). Data collection began when the tone sounded, and was automatically terminated 2 sec later.

In the first of three blocks of experimental trials, each subject was instructed to open her eyes upon hearing the tone, reach out with the right hand, and pick up the target object using the thumb and index finger. The interval between object viewing and the signal to initiate movement was approx. 2 sec in length.

Before beginning the second condition, each subject was instructed to look at the object during the 5 sec viewing period and try to remember what it looked like and where it was located during the 2 sec delay period which would follow. While the subject's eyes were closed during the delay interval, the object was removed from the table surface. This time, when the tone sounded the subject was to open her eyes, reach out, and pretend to pick up the particular object she had seen during the viewing period, *as if it was still physically present*.

In the final condition the delay period was increased to 30 sec but in every other respect the procedure was the same as in the second condition. Subjects were instructed that during this longer delay period they should concentrate on remembering the object's location and shape, in order to pretend to pick it up as though it was actually present at the sound of the tone.

Each condition formed a block of trials consisting of four presentations of each object at each location, for a total of 36 trials. The particular object used and its distance from the hand's start position were varied across trials in a pseudorandom order, with the stipulation that no more than three consecutive trials could be to the same object or location. Three practice trials preceded each condition.

The order of the conditions remained fixed across Ss. This ordering introduced bias against the hypothesis that the experimental conditions would differ, since each subject had the opportunity to 'practice' reaching to the test objects before she was required to pantomime, which should have biased the results toward normal-looking kinematic profiles. Fatigue was not expected to be a factor as previous work in our laboratory has shown that movement kinematics remain very stable across lengthy test sessions of this sort [23].

Results

Performance of normal subjects. The same dependent measures defined in Experiment 1 were studied in this and subsequent experiments. As before, for each subject, means were calculated for each of the dependent measures from the four repetitions of each type of trial. To assess general trends in the performance of the normal subjects, these data was submitted to a series of 3 (Reach Type: normal grasp, 2 sec delay pantomime, 30 sec delay

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*The authors would like to thank D.F. for her patience and cooperation during the collection of the data reported here.

Table 3. Effects of varying test condition on a variety of kinematic measures in Experiment 2 ($n=10$). Scores are summed over the 3 object distances and 3 object sizes. S.E. of mean values in parentheses. Contrasts were tested at the 0.05 level of significance

	Normal grasp	2 sec delay	30 sec delay	Contrasts	*F* statistic
Peak velocity (cm/sec)	84.5 (2.36)	78.9 (2.26)	76.2 (2.45)	OP>2=30	$F(1.43, 12.86)=8.43$, $P<0.01$
Duration (msec)	686 (15.4)	795 (17.3)	844 (17.7)	OP<2=30	$F(1.63, 14.63)=7.57$, $P<0.01$
% Time to peak velocity	43.8 (0.76)	38.9 (0.92)	38.8 (0.79)	OP>2=30	$F(1.68, 15.08)=4.5$, $P<0.05$
Max. wrist height (mm)	133 (2.3)	148 (2.9)	150 (3.3)	OP<2=30	$F(1.34, 12.10)=7.35$, $P<0.05$
% Time to max. wrist height	51.1 (0.85)	46.3 (0.97)	46.7 (0.97)	OP>2=30	$F(1.23, 11.06)=5.59$, $P<0.05$
Max. aperture (mm)	93 (1.1)	85 (1.6)	85 (1.5)	OP>2=30	$F(1.4, 12.58)=5.39$, $P<0.05$

pantomime) × 3 (Object Width: 2.5 cm, 3.5 cm, 5 cm) × 3 (Object Distance: 20 cm, 30 cm, 40 cm) univariate ANOVAs, with repeated measures on all three factors.

The performance of the control subjects was consistent with that of the subjects described in Experiment 1. Thus, while the pantomimed actions performed under the two different delays were virtually identical, striking differences were observed in movement kinematics between pantomimed actions and normal grasping responses. These effects are summarized in Table 3, which also includes information about significant pair-wise contrasts. In Fig. 1 data from representative single trials are presented graphically to demonstrate some of the effects described below.

In both delay conditions, peak resultant velocity was lower and movement duration increased relative to when the object remained in view. Most of the increase in movement duration was due to subjects devoting a greater proportion of total movement time to deceleration (i.e. they spent proportionately less time accelerating to peak velocity in the two delay conditions). (This effect was statistically significant only at the two closest target locations [Reach Type × Object Distance: $F(2.5, 22.46)=5.45$, $P<0.01$].) There was, however, also a small increase in the absolute amount of time spent attaining peak resultant velocity in the 30 sec delay condition, relative to the condition in which the object remained on the table surface.

In addition, the wrist followed a very different path in the two delay conditions than it did when the object could be seen, rising higher above the table surface during pantomimed actions. Despite this, subjects spent proportionately less time raising their hands and more time lowering them in the two delay conditions.

Maximum grip aperture was also significantly smaller during pantomimed actions than during normal reaches, regardless of the length of the delay period. This effect did not interact with object size, indicating that subjects continued to scale the maximum opening of their hand for object size in all three test conditions (see Fig. 2). As can be seen in the representative traces shown in Fig. 1, however, the grip aperture profiles were somewhat flattened relative to normal grasping responses. Thus, subjects did not open and then close their hands as in normal target-directed movements [15]; instead, they appeared to open

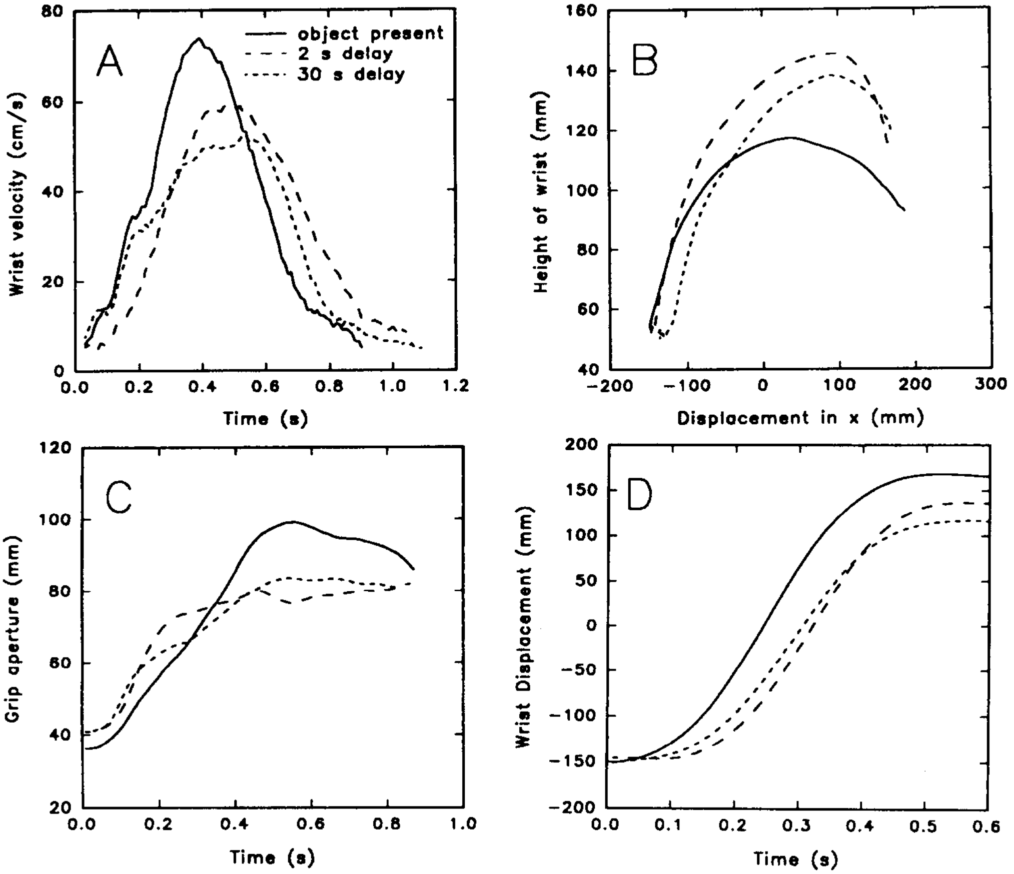

Fig. 1. Representative traces from individual trials demonstrating the effects of imposing a delay of either 2 or 30 sec between object viewing and execution of a pantomimed response on the movements made by the 10 neurologically-intact subjects in Experiment 2. These included: (A) reduction in peak velocity and increase in movement duration; (B) increase in maximum wrist trajectory height; (C) flattening of the grip aperture profiles; and (D) undershooting of target location (values on the *y* axis represent wrist displacement in the forward/backward dimension, relative to the origin which lay at the midline start position).

their hands to a predetermined aperture and then attempt to hold that aperture constant for the duration of the movement.

While mean wrist displacement obviously increased for more distant targets in all test conditions, this effect interacted with Reach Type such that subjects tended to undershoot true target location in the two delay conditions relative to when the object remained present. (This effect was statistically significant only for the two nearer target locations [Reach Type × Object Distance: $F\,(1.68,\ 15.13)=4.37$, $P<0.05$].)

As can be seen in Table 4, increases in *object width* led to the expected increase in maximum grip aperture and in the time taken to attain maximum grip aperture in-flight. In addition, movement duration and wrist displacement increased significantly as object width increased. Increasing *object distance* led to increases in peak resultant velocity and maximum grip aperture, and in the time taken to achieve each of these maxima. However, subjects' normal

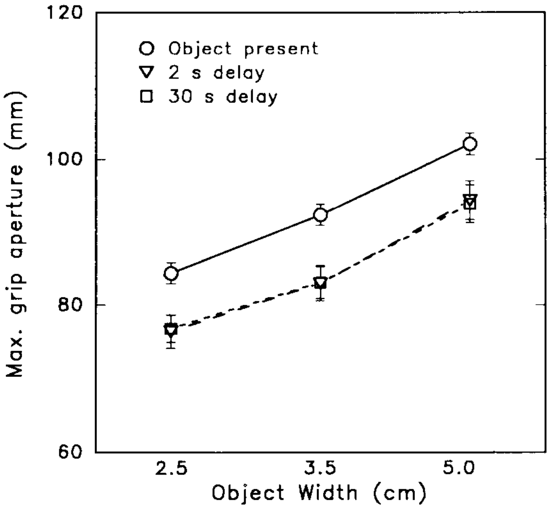

Fig. 2. Mean values of the maximum aperture (in mm) between the index finger and thumb for each of the three target objects in the three testing conditions for the 10 neurologically-intact subjects in Experiment 2. (Error bars represent the standard error of mean values.)

tendency to increase the opening of the hand when reaching to a more distant target [14], while present in all three test conditions, was somewhat exaggerated when a delay of 2 or 30 sec was imposed between object viewing and movement execution [Reach Type × Object Distance: $F(3.16, 28.43) = 5.82$, $P < 0.01$]. In addition, with the obvious increase in wrist displacement seen as target distance increased, there were corresponding increases in maximum trajectory height and movement duration. Finally, the proportion of time spent raising the limb was slightly smaller for closer targets.

Performance of the patient D.F. Close examination of the patient's movement kinematics suggests that reaches in the normal grasping condition were within normal limits in terms of average duration, maximum wrist trajectory height, and peak resultant velocity. These observations are entirely consistent with our earlier report [10]. In addition, despite the fact that D.F. fails to discriminate between the experimental objects in perceptual testing (see Ref. [10] and Table 7, below), when she reaches out to pick up these objects her hand preshapes in-flight in a manner that reflects normal sensitivity to their dimensions. Thus, when an object is visible in front of her, the maximum aperture between her index finger and thumb is scaled as a function of object size as she reaches out to grasp it. This result is shown in Fig. 3(A), which includes raw data for maximum grip aperture for the small and large objects in the normal grasping condition. Note that there is very little overlap between these two sets of scores. It is important to remember that this maximum is achieved well before contact is made with the test object. In other words, it is programmed solely on the basis of the visual information which is currently available.

When a delay is imposed between object viewing and movement initiation, all evidence of anticipatory hand shaping disappears in the patient. This is true even with a delay as short as 2 sec. This result is depicted in Fig. 3(B), in which the raw data from the 2 sec delay condition are presented; in this figure the two distributions overlap completely (the same result was seen with a 30 sec delay). These results are shown even more dramatically in Fig. 4, in which changes in grip aperture during individual reaching trials in the no delay and 2 sec delay

Table 4. Effects of varying object width and distance on a variety of kinematic measures in Experiment 2 ($n = 10$). Scores are summed over the 3 testing conditions (normal, 2 sec delay, and 30 sec delay). S.E. of mean values in parentheses. Contrasts were tested at the 0.05 level of significance

Object width	2.5 cm	3.5 cm	5.0 cm	Contrasts	F statistic
Max. aperture (mm)	79 (1.1)	86 (1.3)	97 (1.4)	$2.5<3.5<5$	$F(1.15, 10.3)=130$, $P<0.001$
Time to max. aperture (msec)	557 (20.8)	593 (20.2)	601 (20.0)	$2.5<3.5=5$	$F(1.5, 13.2)=6.15$, $P<0.05$
Duration (msec)	760 (17.8)	775 (17.9)	791 (18.9)	$2.5<5$	$F(1.8, 16.1)=4.25$, $P<0.05$
Wrist displacement (mm)	171 (9.0)	173 (8.9)	176 (8.8)	$2.5=3.5<5$	$F(1.78, 16.01)=11$, $P<0.005$
Object distance	20 cm	30 cm	40 cm	Contrasts	F statistic
Peak velocity (cm/sec)	60.3 (1.21)	81.1 (1.67)	98.3 (2.16)	$20<30<40$	$F(1.07, 9.59)=108$, $P<0.001$
Time to peak velocity (msec)	262 (4.2)	303 (4.5)	336 (5.7)	$20<30<40$	$F(1.35, 12.18)=47$, $P<0.001$
Max. aperture (mm)	85 (1.5)	85 (1.4)	92 (1.4)	$20=30<30$	$F(1.57, 14.15)=16$, $P<0.001$
Time to max. aperture (msec)	545 (17.6)	543 (19.4)	662 (21.4)	$20=30<40$	$F(1.31, 11.81)=12$, $P<0.01$
Wrist displacement (mm)	73 (1.9)	173 (1.9)	274 (1.5)	$20<30<40$	$F(1.3, 11.8)=3526$, $P<0.001$
Max. wrist height (mm)	122 (1.6)	144 (2.4)	165 (2.8)	$20<30<40$	$F(1.14, 10.23)=74$, $P<0.001$
Duration (msec)	703 (17.4)	788 (18.1)	834 (16.4)	$20<30<40$	$F(1.38, 12.45)=48$, $P<0.001$
% Time to max. wrist height	46.9 (0.87)	48.9 (0.96)	48.3 (1.02)	$20<30=40$	$F(1.78, 16)=6.29$, $P<0.05$

conditions are plotted. A comparison of Fig. 1(C) and the grip aperture profiles of Fig. 4 demonstrates that, while D.F. looks just like a normal subject when she reaches to objects which are continuously present, her anticipatory hand shaping is severely disrupted by the imposition of even short delays. It is important to note that the poor performance during the pantomimed grasp cannot be explained by the fact that visual feedback about the target object is not continuously available in this condition. In previous testing, we have shown that D.F., like normal subjects, continues to show appropriate scaling of her grip aperture during 'open-loop' testing in which the subject's view of the target and the moving hand is prevented after movement onset (unpublished observations).

Despite the apparently rapid loss of size information in the delay conditions, D.F. continues to remember where the object had been located relatively accurately. In fact, not only did peak resultant velocity and movement amplitude continue to be scaled for object distance following a delay (see Fig. 4), but her reach endpoints were quite comparable to those of the subjects tested in the present study, although a tendency to undershoot all targets was noted in the 30 sec delay condition. It is difficult to draw any inferences from these data, however, because the differences in position (which ranged from 10 to 20 cm) were an order of magnitude greater than the differences in object size.

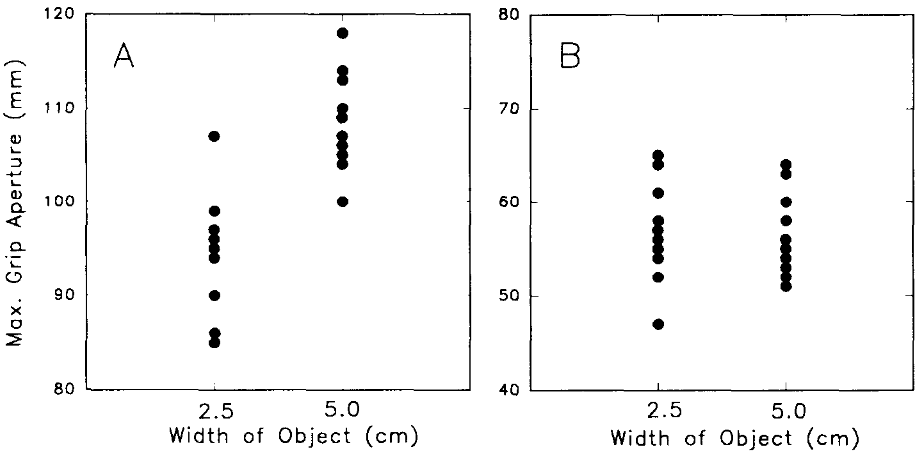

Fig. 3. Raw data showing the range of maximum grip aperture scores for individual reaching trials directed to the small (2.5 cm wide) and large (5.0 cm wide) target objects for the patient D.F. in the no delay (panel A) and 2 sec delay (panel B) conditions of Experiment 2. Note that only in the latter condition is there a substantial degree of overlap in these two sets of scores.

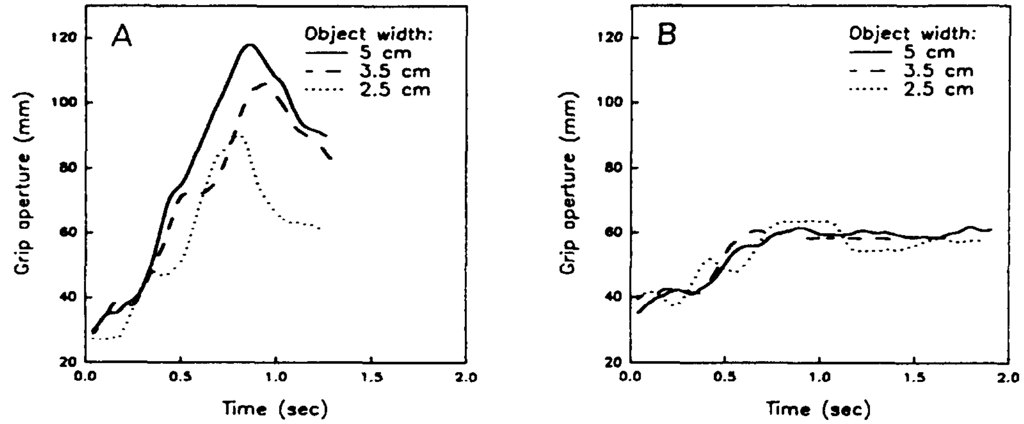

Fig. 4. Representative traces from individual reaching trials in the no delay (panel A) and 2 sec delay (panel B) conditions for the patient D.F. in Experiment 2. Note that, while peak velocity and movement amplitude continue to be scaled for target distance during the delay condition, all evidence of anticipatory hand shaping is lost. Thus in the delay condition, unlike the no delay condition, there is no relationship between the maximum opening of the patient's hand in flight and the size of the target object.

Discussion

The results from the normal subjects replicated those of Experiment 1 and confirmed our prediction that there would be striking differences between reaches generated in 'real time' and pantomimed responses to 'remembered' targets. This suggests that normal visuomotor programs were not being implemented during pantomimed grasping movements. Instead, as we proposed earlier, subjects may have been extracting the information needed to scale their grasp from a stored 'percept' of the object rather than from the transformations provided by the usual on-line visuomotor networks.

Support for this idea came from the performance of the patient D.F. on the delay tasks. Even after the 2 sec delay, D.F. appeared to have 'lost' all information about object size needed to preshape her hand in flight. Of course, this was to be expected since D.F. had no 'percept' of the object in the first place. Thus, when no object was present to drive her real-time visuomotor control systems, she could not fall back on the stored information about object size that was available to normal subjects.

As we have argued above, for perceptual systems (i.e. those involved in visual learning and recognition), a retention interval of 2 sec is trivial. Clearly we are capable of remembering the characteristics of objects we have seen only once for extremely long periods of time. The visuomotor coordinates needed to program a given movement, however, may have to be updated even over intervals as short as 2 sec as the relative positions of the observer and the object change. Thus it would be counterproductive to store these coordinates for any significant period of time; far better that they be calculated immediately before each action occurs. It is perhaps not surprising, then, that there was virtually no difference between the 2 sec and the 30 sec delay conditions for either the normal subjects or the patient.

The control of manual prehension depends on visuomotor systems that not only operate in real time but work with coordinate systems that locate the object in egocentric frames of reference. Thus, we would expect them to be ill-equipped to deal not only with a *temporal* delay between 'seeing' the object and directing an action towards it but also with a significant *spatial* transformation of the required output coordinates. For example, we might expect that requiring a subject to pantomime a grasping movement *beside* an object, as opposed to requiring her to grasp it directly, would not invoke normal visuomotor control processes. In short, the kinematics of such spatially-displaced responses might be expected to resemble those of the temporally-delayed responses described in Experiments 1 and 2. Moreover, since these pantomimed responses would also presumably be driven by perceptual representations of the target object, we would expect the patient D.F. to be unable to perform them convincingly. These possibilities were tested in Experiment 3.

EXPERIMENT 3

Neurologically-intact subjects

Subjects. The subjects were 10 right-handed females ranging in age from 19 to 36 years (mean age 23.4 years). None of the subjects had prior experience with the task. All subjects were students at the University of Western Ontario and all were paid for their participation.

Apparatus and procedure. The apparatus was identical to that used in Experiment 2. There were two experimental conditions, which were run in a counterbalanced order across subjects. In one condition, a given object was centered over one of three possible locations 20, 30 or 40 cm beyond the start key, along the midline. In the other condition, the right end of the object was placed flush with an imaginary line parallel to but 7.5 cm to the left of the midline, from the subject's perspective (see Fig. 5). The center of the object's short axis lay 20, 30 or 40 cm directly in front of a point 7.5 cm to the immediate left of the start key.

In each condition, the object used and its location was varied in a pseudorandom order across trials, with the stipulation that no more than three consecutive trials were to the same distance or object. In both conditions, each object was presented four times at each distance, for a total of 36 trials.

Between trials, subjects sat with eyes closed. On a verbal prompt from the experimenter, the subject opened her eyes and fixated the target object. After a viewing period lasting approx. 5 sec, a tone sounded signalling the beginning of the data collection period. In the condition involving actual grasping, subjects were instructed to reach out and pick up the target object in response to the auditory signal. In the spatial-displacement condition, subjects were instructed to imagine that an object identical to the one on their left was positioned at the same distance from them, but along the midline. They were then to pantomime a grasping movement to that imagined object and pretend to pick it up as if it were physically present. Three practice trials preceded each test condition.

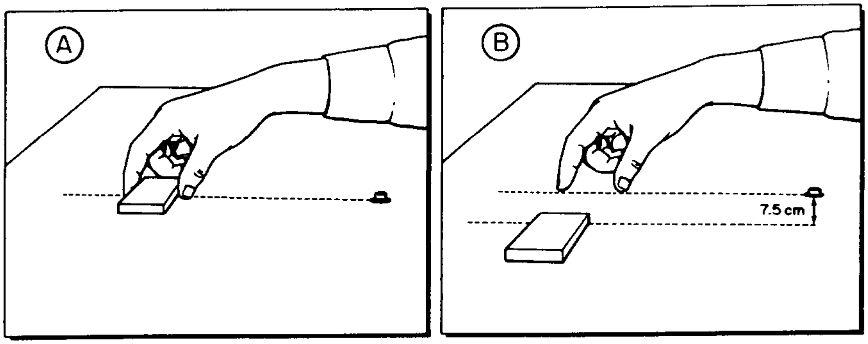

Fig. 5. Illustrations of the two experimental conditions used in Experiment 3. In the first condition (panel A) the subject reached out and grasped an object presented along the midline. In the second condition (panel B) the subject viewed an object presented slightly off the midline and was then required to imagine an identical object at midline which she was to pretend to grasp.

Table 5. Effects of varying test condition on a variety of kinematic measures in Experiment 3 ($n = 10$). Scores are summed over the 3 object distances and the 3 object sizes. S.E. of mean values in parentheses

	Normal grasp	Spatial-displacement	*F* statistic
Peak velocity (cm/sec)	77.3 (1.68)	74.6 (1.76)	$F(1, 9) = 6.35$, $P < 0.05$
Max. wrist height (mm)	133 (2.3)	144 (2.5)	$F(1, 9) = 12.66$, $P < 0.01$
Duration (msec)	784 (17.5)	848 (18.3)	$F(1, 9) = 16.33$, $P < 0.005$
Max. aperture (mm)	74.1 (1.30)	66.5 (1.22)	$F(1, 9) = 8.10$, $P < 0.05$

Results

This experiment involved a series of 2 (Reach Type: Grasp vs Pantomime) × 3 (Object Width: 2.5 cm, 3.5 cm, 5 cm) × 3 (Object Distance: 20 cm, 30 cm, 40 cm) univariate ANOVAs with repeated measures on all factors.

As can be seen in Table 5, relative to reaches directed toward real objects, mimed actions had lower peak resultant velocities, higher maximum trajectory heights, and longer durations. In addition, maximum grip aperture was significantly smaller in the pantomime condition than in the condition involving normal grasping.

Once again, many of the effects which resulted from the manipulation of object size and distance were replicated (see Table 6 for means, test statistics, and significant contrasts). Increases in *object width* were associated with increases in peak resultant velocity, maximum grip aperture (and the time at which this maximum occurred), and movement duration. There was also a trend ($P = 0.05$) for the wrist to be raised higher off the table surface when reaching toward larger objects. Increases in *object distance* were associated with increases in peak resultant velocity, maximum grip aperture, and maximum wrist height and the times at which each of these maxima was attained, and with increases in movement duration.

Table 6. Effects of varying object width and distance on a variety of kinematic measures in Experiment 3. Scores are summed over the two testing conditions (normal grasp and spatial displacement). S.E. of mean values in parentheses. Contrasts were tested at the 0.05 level of significance

Object width	2.5 cm	3.5 cm	5.0 cm	Contrasts	*F* statistics
Peak velocity (cm/sec)	75.3 (2.14)	75.8 (2.07)	76.8 (2.15)	$2.5<5$	$F(1.93, 17.35)=4.75$, $P<0.05$
Max. aperture (mm)	61 (1.1)	69 (1.1)	81 (1.4)	$2.5<3.5<5$	$F(1.22, 10.95)=518$, $P<0.001$
Time to max. aperture (msec)	645 (19.9)	666 (20.6)	705 (19.3)	$2.5<3.5<5$	$F(1.46, 13.18)=9.97$, $P<0.01$
Duration (msec)	795 (22.1)	817 (22.1)	838 (22.7)	$2.5<3.5<5$	$F(1.66, 14.90)=16.2$, $P<0.001$
Max. wrist height (mm)	137 (3.0)	138 (2.9)	140 (3.1)	Not performed	n.s. $P=0.05$
Object distance	20 cm	30 cm	40 cm	Contrasts	*F* statistics
Peak velocity (cm/sec)	59.9 (0.98)	77.4 (1.42)	90.6 (1.58)	$2.5<3.5<5$	$F(1.21, 10.89)=275$, $P<0.001$
Time to peak velocity (msec)	280 (8.9)	304 (5.3)	339 (5.4)	$2.5<3.5<5$	$F(1.19, 10.69)=28$, $P<0.001$
Max. aperture (mm)	69 (1.6)	69 (1.6)	72 (1.7)	$2.5=3.5<5$	$F(1.86, 16.75)=9.04$, $P<0.005$
Time to max. aperture (msec)	576 (16.2)	688 (17.7)	752 (19.5)	$2.5<3.5<5$	$F(1.51, 13.58)=31$, $P<0.001$
Max. wrist height (mm)	116 (1.5)	138 (1.6)	162 (2.0)	$2.5<3.5<5$	$F(1.16, 10.4)=212$, $P<0.001$
Time to max. wrist height (msec)	348 (8.9)	368 (6.2)	405 (6.9)	$2.5<3.5<5$	$F(1.20, 10.76)=27$, $P<0.001$
Duration (msec)	693 (15.9)	822 (19.0)	934 (20.0)	$2.5<3.5<5$	$F(1.17, 10.57)=87$, $P<0.001$

The patient D.F.

A similar experiment to that described above was carried out on the patient D.F., 24 months after the study described in Experiment 2.* Some minor changes were made to the procedure at this time, as noted below.

Apparatus and procedure. The apparatus for this experiment was identical to that described above, except that three additional objects were included, matched for surface area with the original three but differing in their dimensions. The full set of objects, then, had the following surface dimensions: 5 × 5 cm; 4.5 × 5.5 cm; 4 × 6.25 cm; 3.5 × 7.15 cm; 3 × 8.3 cm; and 2.5 × 10 cm.

D.F., like the controls, began each trial with the tips of her right index finger and thumb touching and depressing the start key, and with eyes closed. On a verbal prompt from the experimenter, D.F. opened her eyes and waited for a 'ready' signal to initiate her grasping or pantomimed response. This signal was given after a viewing period of approx. 2 sec.

In the normal grasping condition, target location was restricted to a single location, 30 cm in front of the hand's midline start position. In the pantomime condition, target objects were always placed 30 cm beyond a point 7.5 cm to the left of the midline start key, as described above. In this condition, D.F., like the normal subjects, was instructed to imagine (as best she could) that an object identical to the one on her left was positioned at the same distance from her, but along the midline. She was then to pantomine a grasping movement to that imagined object and pretend to pick it up as if it were physically present.

The two conditions were run in separate blocks, with the normal grasping responses run first to bias against the

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*The authors would like to thank K. Murphy for her assistance in collecting and analyzing the data for this experiment.

hypothesis that D.F. would be worse during pantomimed trials. In each block, each object was presented six times, in random order, for a total of 36 trials.

Results

Since target location was not varied in the study involving D.F., the variable of greatest interest is maximum grip aperture. Although D.F.'s ability to scale grip aperture in the present pantomime condition was marginally better than it had been in the delay condition of Experiment 2, her responses were nonetheless extremely variable compared to her normal grasping movements. Indeed, as Fig. 6(B) shows, there was considerable overlap in the maximum apertures produced during pantomimed movements carried out, for example, during reaches to the narrowest (2.5 cm) and widest (5.0 cm) of the target objects. In contrast, there was no overlap in these scores during natural grasping movements directed at these same objects (Fig. 6A).

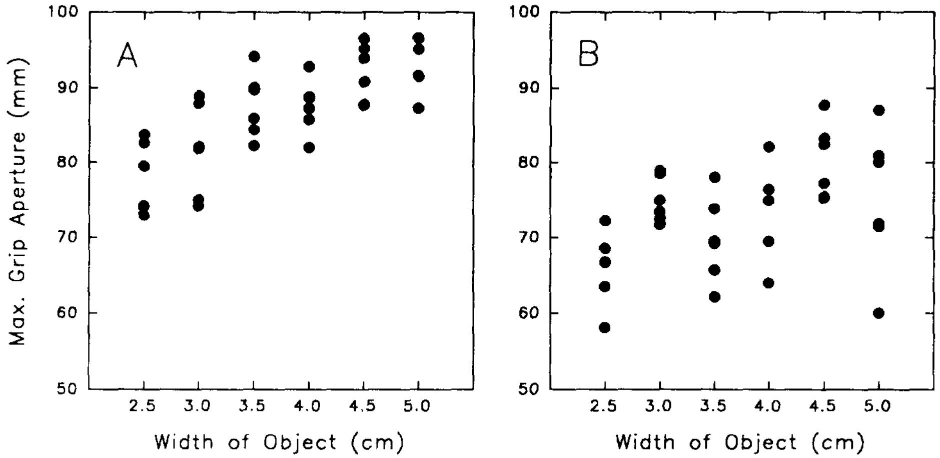

Fig. 6. Raw data from the patient D.F., showing the range of maximum grip aperture scores for individual reaching trials directed to the various target objects used in Experiment 3 during target-directed (panel A) and pantomimed (panel B) grasping responses. Note that in the latter condition there is substantially more variability and overlap in the scores.

Discussion

Despite the fact that no delay period was imposed and the target object was always visible in both conditions, pantomimed reaches performed by the normal subjects in the present study resembled the pantomimed reaches described in Experiments 1 and 2 in a number of respects. Relative to reaches directed toward real objects, the spatially-displaced pantomimed reaches had lower peak resultant velocities, followed more curvilinear trajectories, and lasted longer. In addition, as had been observed in the delay conditions of Experiments 1 and 2, maximum grip aperture was significantly smaller in the pantomime condition than in the condition involving normal grasping.

These data, taken together with the poor performance of the patient D.F. on the pantomime task, lend support to the suggestion that asking subjects to produce spatially-displaced pantomimed grasping movements forces them to rely on 'perceptual' information about the objects, rather than on the sources of information that are normally utilized in the automatic guidance of visuomotor acts. While it is possible that subjects were invoking some sort of 'imaging' strategy to guide their pantomimed responses both in the delay conditions of Experiments 1 and 2 and in the spatially-displaced condition of the present experiment, it is also possible that some other strategy, perhaps one that was more verbal in nature, was being used to code object size. No matter what the strategy was (and different strategies might have been used by different subjects), it seems likely that the use of that strategy depended, at least initially, upon an explicit perceptual representation of the target object. Furthermore, consistent with the proposal of Goodale and Milner [9], the construction of that perceptual representation probably depends on rather different neural machinery than that involved in normal visuomotor control since, in both the present experiment and in Experiment 2, the patient D.F. was unable to perform the pantomime task as well as normal subjects (even though she is quite capable of producing well-scaled target-directed actions).

Of course, it was possible that the difficulty D.F. experienced with these pantomime tasks had less to do with her perceptual impairment than with a problem in: (a) constructing or maintaining mental images of the target objects; and/or (b) understanding the task demands. We would have additional support for the conclusion that D.F. fails on the pantomime tasks because of her perceptual deficit if we could show that her performance improves substantially when she is not required to *construct* a percept but can instead draw on information she is told about objects, or on her general knowledge (long term memory) about objects, in order to guide her pantomimed actions. These predictions were tested in a final series of experimental tasks.

EXPERIMENT 4

Method

Neurologically-intact subjects. Neurologically-intact subjects were the same 10 right-handed females who volunteered for Experiment 2. The mean age of this group was 25.6 years (range 20–36 years). All were students at the University of Western Ontario who were paid for their participation.

Apparatus and procedure. Size estimation tasks. Two size estimation tasks were performed by D.F. and the normal subjects. During the *Perceptually-Driven Size Estimation Task,** each subject wore a pair of goggles to prevent vision of the hand while not obscuring the subject's view of objects placed more centrally on the table. Between trials, subjects sat with eyes closed and with their right index finger and thumb in a pinch formation, depressing the midline start key. While they were in this position, the experimenter positioned one of six different target objects 20 cm directly in front of the hand's start position, with its long axis perpendicular to the midline. Target objects were matched for top surface area, but differed in their dimensions, as follows: 5 × 5 cm; 4.5 × 5.5 cm; 4 × 6.25 cm; 3.5 × 7.15 cm; 3 × 8.3 cm; and 2.5 × 10 cm. Each object was presented four times, in random order.

On a verbal signal from the experimenter, the subject opened her eyes and manually estimated the width of the object placed on the table in front of her. Once the subject indicated that she had positioned her thumb and finger to reflect the (back-to-front) width of the target object, the static positions of two IREDs positioned on the tips of the right thumb and index finger were collected using the WATSMART computer system described earlier. During off-line analysis of filtered data the average three-dimensional distance between these markers during each trial was calculated.

During the *Verbally-Specified Size Estimation Task*, each subject was instructed to sit with her eyes closed and, on a given trial, match the distance between her thumb and index finger to one of six verbally-specified grip sizes. The

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*The *Perceptually-Driven Size Estimation Task* was conducted on D.F. as part of our initial investigation of her in 1990, and her performance on this task was first described in [10]. Data from the control subjects on both the *Perceptually-Driven Size Estimation Task* and the *Verbally-Specified Size Estimation Task* were collected at the time that Experiment 2 was conducted.

Table 7. Correlation coefficients for the size estimation tasks in Experiment 4 (*$P<0.05$)

Subject	Perceptually-Driven Size Estimation Task	Verbally-Specified Size Estimation Task
1	0.8404*	0.5706*
2	0.8807*	0.7976*
3	0.6946*	0.6879*
4	0.9122*	0.8661*
5	0.8793*	0.7623*
6	0.6692*	0.8878*
7	0.8881*	0.8996*
8	0.6609*	0.8067*
9	0.8375*	0.8217*
10	0.8986*	0.6394*
DF	0.1000	0.7800*

grip sizes were specified either in inches or centimetres, according to the preference of each subject, as follows: 5 cm, 4.5 cm, 4 cm, 3.5 cm, 3 cm, and 2.5 cm; or 2.25 in., 2 in., 1.75 in., 1.5 in., 1.25 in., and 1 in. Subjects were instructed to return their thumb and index finger to a pinch position between trials. Each of six grip sizes were specified four times, for a total of 24 trials.

For this task only, grip sizes were measured manually by recording (to the nearest mm) the distance between pen marks placed on the tips of the right index finger and thumb on each trial. This procedure was adopted with the controls to allow for a direct comparison with data collected manually from D.F. during a test session carried out in Italy 4 months earlier.

Pantomime task. This task involved only the patient D.F. On a given trial, D.F. was asked to imagine a variety of *familiar* objects of standard (known) sizes (a pencil, a hazelnut, a table tennis ball, a tangerine, a tennis ball and a grapefruit) and pretend to pick each of them up.* Two pantomimed actions were executed toward each imagined object, and the 12 trials were presented in random order. Next we had her actually grasp each of these objects twice, again in random order. On each trial of both tasks, D.F.'s hand was videotaped at 50 Hz and frame-by-frame analysis was carried out off-line to find the maximum grip aperture that was achieved.

Results

Size estimation tasks. For the *Perceptually-Driven Size Estimation Task*, correlations were calculated for each subject between actual object width and the manual estimates. Data from the *Verbally-Specified Size Estimation Task* were analyzed in the same fashion, with the calculation of a correlation between specified sizes and manual estimates for each subject. Table 7 indicates that all 10 normal subjects showed significant ($P<0.01$) correlations on both tasks. The patient D.F., on the other hand, was unable to estimate the width of an object manually when it was presented visually, even though she could do so when she was told the dimensions she was to indicate.

Pantomime task. When pantomiming reaches to imagined but familiar objects of known size, D.F.'s responses were much like the pantomimed actions of the neurologically-intact subjects described in Experiments 1–3. In particular, under these circumstances D.F. showed appropriate scaling of grip aperture as a function of object size ($r=0.853$, $P<0.01$ for pantomimed grasping movements; $r=0.977$, $P<0.01$ for grasping movements directed toward the actual objects).

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*This experiment was carried out in Scotland, 14 months after the study described in Experiment 2. The authors would like to thank Dr A. D. Milner and Dr M. Harvey for their assistance in collecting and analyzing the data for this experiment.

Discussion

These results clearly indicate that D.F.'s difficulty in the pantomime tasks described in Experiments 2 and 3 is not with pantomime *per se*, but instead reflects her profound inability to construct useful percepts of object features in a 'bottom–up' (sensory-driven) manner.

The fact that D.F. could imagine familiar objects and pantomime movements toward them (despite her profound recognition deficit) suggests that the neural mechanisms supporting image generation are intact in this patient. Consistent with this interpretation of the present findings, in other experiments D.F. has been shown to have no difficulty rotating her hand to match the orientation of an imagined slot, despite being completely unable to match her hand posture to the orientation of a real slot [10]. Similarly, even though D.F. cannot copy the simplest of line drawings, she is able to draw reasonably well from memory, a task which we assume requires mental imagery [22]. Indeed, these and other observations suggest that D.F. has a rather rich 'inner visual life' (manuscript in preparation).

The existence of well-developed imagery skills in D.F. (and other agnosic patients, see Ref. [2]) has important implications for recent accounts of the neural instantiation of visual imagery. In these accounts, it is often argued that there is considerable overlap between systems supporting visual imagery and those underlying visual perception [3, 5, 6]. Indeed, it has recently been proposed that there are two visual imagery systems, which map onto the two cortical visual systems that have been identified in the primate brain [4, 19]. While there may be some merit in these ideas, the present observations suggest caution in postulating too close a correspondence between imagery and perceptual systems. While it is possible that the generation of a mental image can activate perceptual systems in a 'top–down' fashion in patients like D.F., even if low-level visual inputs cannot, it is equally possible that imagery mechanisms are quite independent of the perceptual machinery.

CONCLUSIONS

The fact that D.F. could use imagery to pantomime movements convincingly in Experiment 4 shows that her failure in Experiments 2 and 3 arises from a deficit in perception, not in visuomotor planning or control. D.F.'s difficulty in the delay condition, coupled with the fact that the pantomimed actions of normal subjects were quite different from natural grasping movements, supports our contention that visuomotor control networks operate in 'real time', with little or no memory. This is not to suggest that memory about objects does not influence motor behavior, or that memory is not used to optimize motor performance. After all, we can and do use information about objects, such as their weight, fragility, temperature, and friction coefficients, in planning movements directed at those objects [17]. In addition, we all know that our performance of many motor skills improves with practice. Yet when we plan an action, however well-rehearsed and informed we might be about the intrinsic characteristics of the goal object, we still must compute the instantaneous position and orientation of the target object in egocentric coordinates to execute that action. Here we cannot rely on memory because, of course, the precise position and orientation of that object with respect to our own body coordinates will vary enormously from one occasion to the next. For this and other reasons, it would make good sense for the visual inputs and transformations supporting the visual control of goal-directed actions to be quite independent of those mediating object recognition, which typically require access to stored representations of objects. Indeed, Goodale and Milner [9] have proposed that these two kinds of visual processing are mediated by quite separate cortical visual pathways: a ventral stream mediating the perception and recognition of objects and a dorsal stream mediating the visual guidance of skilled actions directed at those objects. There is no 'general purpose' visual representation to which all thought and action is referred.

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