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The Role of Short-Term Visuo-Spatial Memory in Control of Rapid Multi-Joint Prehensive Movements

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Summary. How memorized visuo-spatial information influences motor control and whether this information is able to replace the feedback processing in cases of visual deprivation was studied using an unrestrained finger- and hand-movement paradigm. Nineteen right-handed subjects were asked to grasp and lift a small block with the index finger and thumb of the right hand, as quickly as possible. The efficiency of motor performance was analysed by measuring the grasping time derived from tangential velocity profiles of the fingertips. The data revealed significantly shorter grasping times under continuous visual guidance than during blind grasping. Grasping times increased under conditions with stepwise prolongation of visual deprivation time prior to the movement onset. The results support the general concept that within the first seconds of visual deprivation, stored visuo-spatial information can partly compensate for the lack of continuous visual feedback.

Key words: Short-term memory – Visuo-motor control – Space representation – Finger movement

Introduction

In natural prehensive movements, visual parameters of the target object (such as location in extracorporeal space, shape and size) define the trajectory of a target movement and represent the basis for a motor program that selects the appropriate feedforward motor commands. Furthermore, during the execution of a goal-directed movement, movement parameters such as duration, velocity profile or terminal precision can also be influenced by current visual input (Jeannerod and Prablanc 1983).

In rapid goal-directed movements, one can assume at least two levels of organization in visuomotor processing: a higher level of motor control based on visual input (open loop) and a lower level of motor control involving detection and correction of the terminal error by a peripheral feedback loop (Megaw 1974). Both levels use visuo-spatial cues of target location, which have to be stored for a defined period of time to be available for movement execution.

In daily motor performance visual information is necessary for programming a distinct individual movement among a large set of goal-directed movements of continuously changing target positions as well as target shapes and sizes. It is likely that this visual information is stored only for a restricted amount of time. So far, little is known about the characteristics of such a visuo-spatial memory. It is of special interest to know how long the specific visuo-spatial cues will be stored in a memory bank and if there is a continuous or abrupt decay of visuo-spatial memory content. Such a decay could express itself in a decreasing accuracy of the motor execution or in a slowing down of the movement to offer time for non-visual feedback processing.

Thomson (1983) found some evidence for internalized visual information stored in short-term memory. He asked blindfolded subjects to walk to a target with different waiting periods before starting to walk. He reported a storage time of approximately 8 s in which subjects could meet the target very accurately. From an additional experiment he postulated that such memory information was available in a general form without connection to a fixed motor program. Gielen et al. (1984) performed experiments with simultaneous eye and arm movements in double-step track-

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ing tasks. From his data he postulated a "common command signal" specifying end-position of movements in parallel working motor systems. This signal was assumed to be freely available, e.g. in a target-oriented internal representation and not coded in specified motor programs.

In order to test the dynamics of visuo-spatial memory, a motor system which has to adapt the motor commands to a nearly infinite number of target constellations is most suitable. This can actually best be achieved with movements of the upper limbs. During a reaching movement, the behaviour of the hand in the immediate vicinity of the target is of particular interest. This is the phase where a switching from a higher to a lower level of motor control could be postulated. The low-level phase in the vicinity of the target is characterized by a low-velocity phase before the contact with the target. Jeannerod (1984) and Wing et al. (1986) reported that the maximum grasp aperture was the beginning of this low-velocity phase. Jeannerod (1984) assumed a centrally patterned link between grasp and transport of the hand towards the target, which lasts until the final grip. Wing et al. (1986) considered only the transport phase and the maximum grasp aperture to be predictive and not to be based on concurrent feedback. He argued that preprogramming uses internalized information about the target and the expected movement accuracy. It is reasonable to postulate a visuo-spatial memory for this type of internalization, which Wing et al. described. The low-velocity phase based on peripheral feedback has to compensate any decreasing accuracy due to a gradual loss of visuo-spatial memory.

It was the aim of the present study to investigate how memorized visuo-spatial information influences unrestrained movements and whether the visuo-spatial memory signal is able to replace feedback processing when a deprivation of visual feedback occurs.

Method

Trajectory data on unrestrained grasping movements were collected using an electromagnetic recording device with slight modifications from the one described by Schönle et al. (1983, 1987). The device consisted of three triangularly positioned transmitter coils which produced an alternating magnetic field of three different frequencies. In a miniature receptor coil (2 mm × 2 mm × 4 mm in size) a voltage signal was induced which provided information about the distance to each transmitter coil. After splitting the signal into its components and conducting A/D conversion, a PDP 11 computer determined the coordinates of the fingers in the two-dimensional plane. Vertical plane trajectories of index finger and thumb during grasping of a rectangular block (Fig. 1A) were recorded by fixing receptor coils at the tips of these fingers. A possible tilt of the receptor coil could be detected and compensated. A deviation of the fingers out of the median plane up to 3 cm did not cause noticeable projection errors. In the central 15 cm × 15 cm working space, an accuracy of 0.5 mm was achieved. Temporal resolution of trajectories was 4 ms by choosing a sample frequency of 250 Hz. Since the recording system's noise was low, the spatial movement path data (x–y data) did not need to be filtered. The tangential velocity was computed by the slope of a linear regression line within a window of 11 sample points that represented a low-pass filter with a cut-off frequency of 23 Hz.

A total of 19 right-handed subjects participated in this study. The age distribution ranged from 19 to 45 years. Fourteen subjects were male and 5 female. The subjects' task was to grasp and lift a small block (1 cm × 1 cm × 3 cm) with the index finger and thumb of the right hand as quickly as possible (see Fig. 1) and to withdraw it to the starting position. All observed movements started from exactly the same point marked by a pin. Subjects touched the pin with their index finger and thumb before starting. Withdrawal ended by placing the block on top of the starting pin. The starting position of the finger tips was located at a direct distance of 20 cm from the target. The recording lasted 2 s and was initiated by an auditory stimulus which informed the subject to start the movement. After performing 10 practice trials with visual guidance, 32 subsequent trials were performed in a random fashion with 8 different conditions. Condition 1 permitted complete visual control; in conditions 2–8 subjects had to close their eyes and to remain so until the grasping movement was terminated. In condition 2 there was only a short delay between closing of the eyes and starting signal (about 1 s). In conditions 3–8 an unfilled interval (without mental distraction) of 5, 10, 15, 20, 30 and 40 s was set before release of the starting stimulus. A trial was not included in the evaluation if the target was missed.

Paths of index finger and thumb tip were displayed and the tangential velocity was computed. Since most subjects were grasping with curved movement paths, the tangential velocity did not reach a zero value. The grasping time was defined as the period in which the tangential velocity was below a level of 40 cm/s (see Discussion). The total movement time was calculated from the first deflection of the velocity curve (indicating the 20 cm forward movement) to the end of the backward movement (when the target block was carried back these 20 cm). Thus the total movement time included two 20-cm ballistic movement components and the grasping time between these ballistic phases. None of the joints of the upper limb was restrained by the apparatus set-up or by task instructions.

Results

Figure 1 demonstrates the experimental set-up, with trajectories and tangential velocity profiles of index finger and thumb during a grasping movement. To permit a temporal comparison of movement events between the two fingers, arrows 1–4 indicate identical time markers. The path curves (Fig. 1C) indicate the movement of both index finger and thumb during target approach, grip, and withdrawal. In this example at time marker 1, the preshaping (opening of the finger grip during target approach) was slightly asymmetrical. The distance to the target was smaller for the index finger than for the thumb. Therefore, the grasping of the target object required a larger adjusting movement of the thumb between time markers 1 and 4. This asymmetry caused a velocity peak of the thumb in

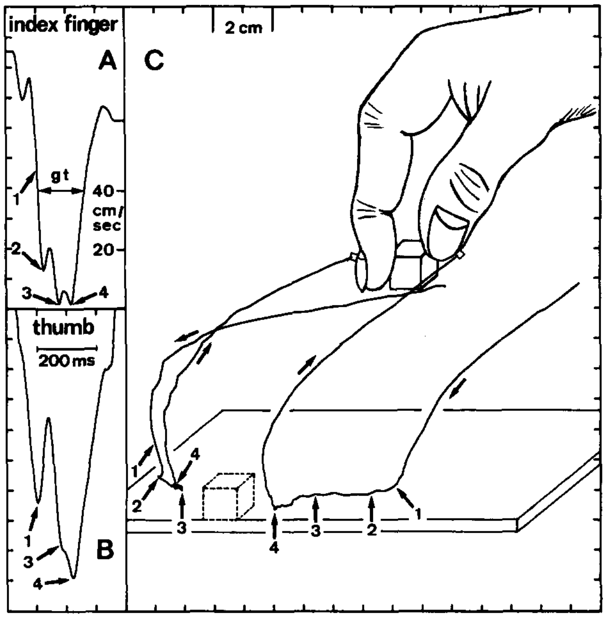

Fig. 1A–C. Trajectories of index finger and thumb during target approach, grip, and withdrawal. *Arrows 1–4* indicate corresponding time markers in the volocity profiles of index finger (**A**) and thumb (**B**) and the path curves of both fingers (**C**) during grasping. The grasping time was defined as the width of the velocity valley at a 40 cm/s level [grasping time *(gt)* in **A**]

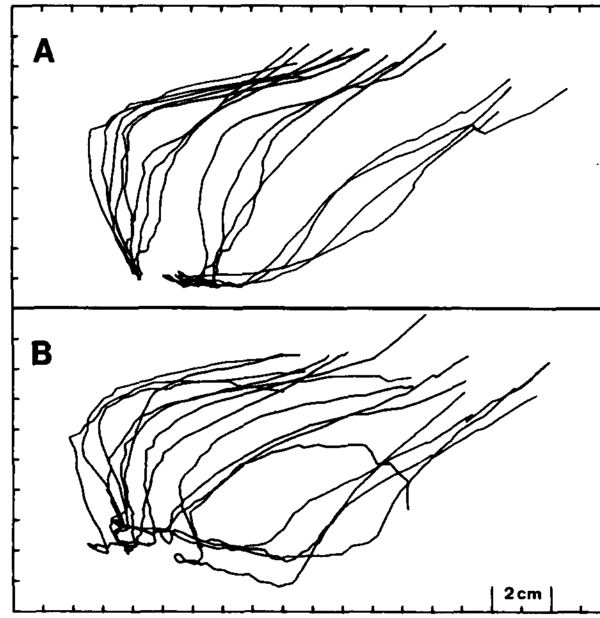

Fig. 2. Superposition of trajectories of four grasping movements of one representative subject with eyes open (**A**) and eyes closed 20 s prior to the onset of each movement (**B**)

Fig. 1B (between time markers 1 and 4), while the index finger remained in the target vicinity (time markers 2–4). Immediately afterwards, contact with the target was made at time marker 4 and the target object was lifted and removed. Even during the first contact with the target the velocity of the thumb movement did not decrease to zero; rather, the thumb tip followed a slightly curved path.

Figure 2 illustrates the spatial movement path of four subsequent grasping movements of one representative subject. In Fig. 2A, continuous visual control was allowed. In Fig. 2B, the subject was requested to keep his eyes closed for an interval of 20 s before grasping blindly. Comparison with Fig. 2A demonstrates the increased variability of movement paths when vision was precluded.

To obtain the temporal aspects of the grasping movements under the tested conditions tangential velocity profiles were computed. The velocity profiles of both index finger and thumb are demonstrated for one representative subject in Fig. 3. A velocity minimum occurred during the approach and the first contact with the target. In the majority of movements, a zero velocity at the target was not reached (since movements followed a slightly curved path). In particular, in conditions with a long delay between the end of permanent visual feedback and blind grasping, one or more lower velocity peaks were seen next to the velocity minimum (Fig. 3E, F). These are apparently equivalent to small adjusting movements. The grasping time was defined as the width of the velocity valley at a 40 cm/s level. The borders of these velocity valleys consisted of steeply decreasing and increasing velocity slopes, which indicated the decelerated ballistic movement toward the target and accelerated backward movement. The ballistic reaching movements were performed with a peak velocity of up to 200 cm/s.

Statistical analysis of the 19 subjects yielded a mean total movement time of 707 ± 150.8 (SD) ms, with the fastest subject requiring 612 ± 65.6 ms, and the slowest 847 ± 167 ms. One-third of this time represented the duration of the ballistic forward movement (233 ± 38 ms mean for all subjects; 192 ± 27 ms, fastest subject; 269 ± 29 ms, slowest subject). A single-factorial analysis of variance revealed a main effect for subject on the total movement time ($F = 24.9$; $P < 0.0001$). Similar effects were produced by the subjects on the duration of the ballistic forward movement ($F = 36.3$; $P < 0.0001$) and the grasping time ($F = 11.58$; $P < 0.0001$).

The conditions of visual deprivation and the increased skill during the experiment could also be a source of variance. To evaluate whether or not there was an effect of skill, the recording session of 32 trials was divided into an initial part of 16 trials and a more skilled part, trials 17–32. A 2 × 8, two-factorial (session half × visual condition) analysis of variance showed major effects of skill ($F = 5.70$; $P < 0.02$) and of visual conditions ($F = 6.47$; $P < 0.001$) on the total movement time. These effects seemed to influence different

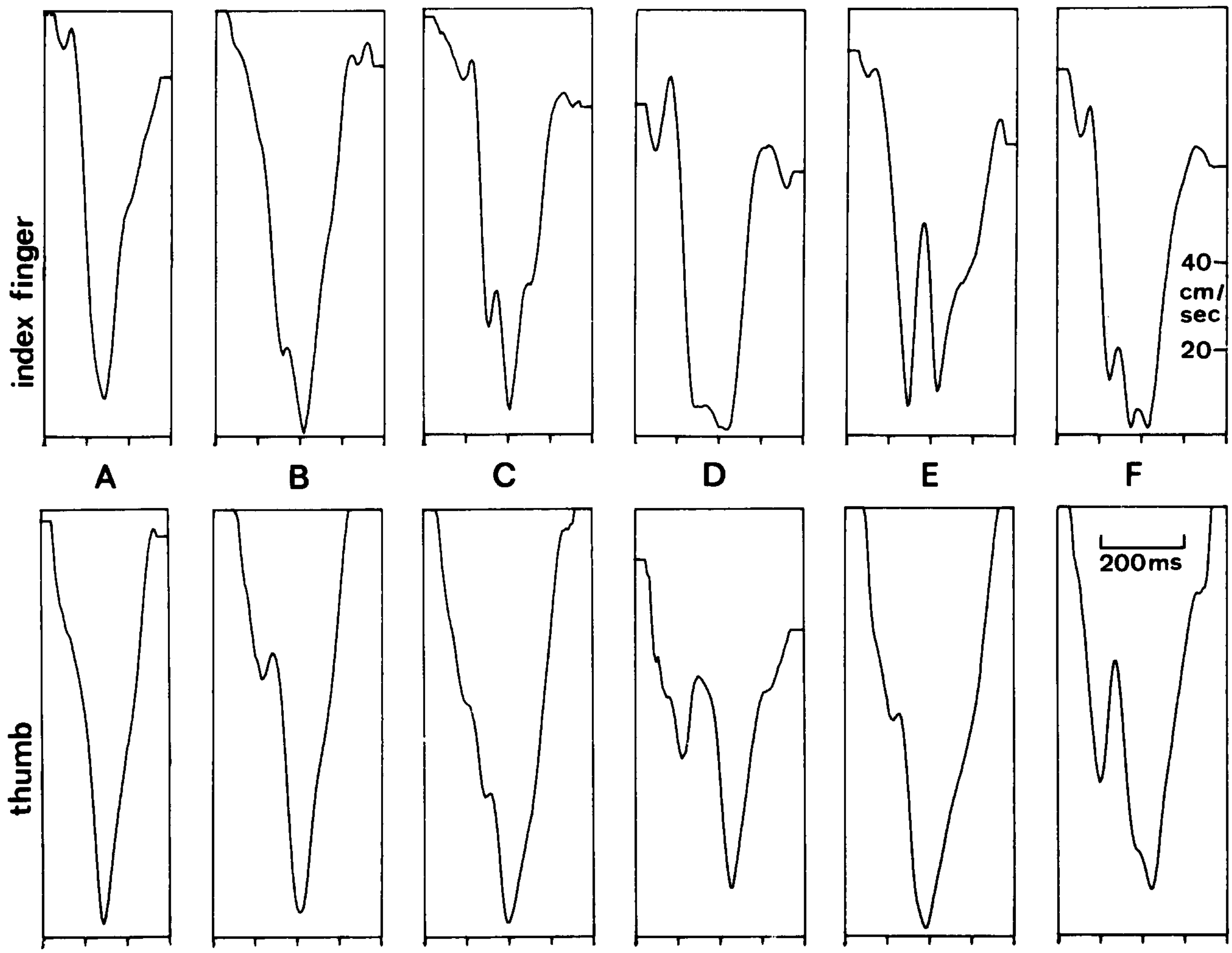

Fig. 3. Velocity profiles during grasping of index finger *(upper row)* and thumb *(lower row)* of one subject with eyes open (column **A**) and eyes closed 1, 5, 10, 20, 40 s prior to movement onset (columns **B, C, D, E, F**). The velocity minimum indicates contact with the target block

components of the total movement time. Skill produced a major effect on the duration of the ballistic forward movement ($F = 30.0$; $P < 0.0001$), whereas the visual conditions did not alter the forward movement time significantly ($F = 1.66$; n.s.). In contrast, the different visual conditions represented the major source of variance of the grasping time ($F = 9.97$; $P < 0.0001$), whereas skill did not influence the grasping time significantly ($F = 1.77$; n.s.). No interactions between skill and visual conditions were found for any of the dependent variables (total movement time, forward movement time, grasping time).

Figure 4 illustrates the function of mean grasping times depending on visual conditions. Under permanent visual control the average of all 19 subjects was 55 ± 31 ms (index finger) and 55 ± 23 ms (thumb). In the conditions with increasing periods of eye closure the observed grasping times progressively increased. The differences between the grasping time under visual guidance versus blind conditions were significant at the $P < 0.002$ level. Under conditions without vision, a reproducible relationship between grasping times and blind intervals was obvious. The mean grasping time of 196 ± 65 ms for the index finger and 195 ± 70 ms for the thumb after a 40-s blind delay turned out to be significantly longer ($P < 0.03$) than mean grasping times after the shorter delays of 1, 5, 10 and 15 s. The mean grasping times after shorter delays ranged from 106 to 137 ms (index finger) and from 99 to 130 ms (thumb). Interestingly, there was no clear difference between grasping times within the three conditions without vision at a delay of 5, 10 and 15 s ($P > 0.25$).

A total of 35 trials could not be included in the statistical analysis of grasping times. For 19 of these trials, the subjects did not keep their eyes open or closed, as required, during the entire movement. A primary task failure in the strict sense occurred in only 16 cases. In most cases following such a failure, the target block

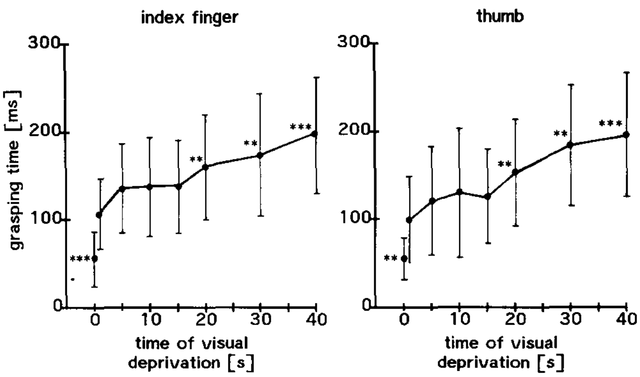

Fig. 4. Grasping times of index finger *(left side)* and thumb *(right side)* versus time of visual deprivation of the target. Mean values *(solid lines)* and standard deviations *(vertical bars)* of a total of 19 subjects. Significant differences to the condition of closed eyes with 1 s delay before movement initiation are indicated with ** ($P < 0.01$) and *** ($P < 0.001$). Note the significant difference of grasping times obtained with eyes open (0 s) as compared with eyes closed 1 s prior to the onset of the movement. Furthermore there was a significant difference of grasping times when blindfolded movements with 1 s visual deprivation time were compared with those of 20, 30 and 40 s of visual deprivation

was picked up at a second grasp 200 ms later. Because of the small number, no statistical analysis was performed on error data.

To estimate the coordination between index finger and thumb, a correlation analysis of separately measured grasping times of both was undertaken. All conditions were combined, yielding 573 measurements (19 cases × 32 trials − 35 failed grasps) each for both index finger and thumb. A correlation and *t*-test yielded a positive correlation ($r = +0.88$; $P < 0.0001$). The slope of the corresponding regression line is +0.97, indicating that grasping times of index finger and thumb are identical in most cases. This result indicates that an asymmetrical grasp was quite rare. As illustrated in Fig. 1, such an asymmetrical grasp caused a long grasping time of one finger (e.g. index finger), and a short grasping time of the other (e.g. thumb).

Discussion

The finding of a prolonged grasping time due to an increased blind interval raises the question whether altered motor control could be the reason. Since during blind movements a direct visual feedback or an updating of the visuo-spatial memory is impossible, the only sources of information to control the required movement can be the tactile and kinaesthetic feedback and the memorized visuo-spatial information. Kinaesthetic information and tactile feedback alone are poor candidates for accuracy control because they need a considerable processing and conduction time until they are availalbe for error correction, which slows down the grasping.

It is reasonable to assume that the observed grasping movements which had to be performed as fast as possible were controlled bimodally by kinaesthesis and visuo-spatial memory. Tactile and kinaesthetic feedback have to control the final exploring of the target location if no other feedback is available, particularly if the eyes are closed. But even without vision some grasping movements were performed so quickly (grasping time below 100 ms), that kinaesthetic feedback on its own cannot adequately explain precise motor control. Thus it is necessary to postulate a visuo-spatial memory as another source of information and independent from a simultaneous feedback signal. The collaboration of kinaesthetic feedback and visuo-spatial memory should be most evident near the target, where the low-level phase of motor control (see Introduction) required a feedback mode.

In this experiment the grasping time, i.e. the time the subject's hand was in the immediate vicinity of the target, was chosen as the main parameter for providing information on visuo-spatial memory, as well as on feedback processing. Grasping time was defined as the time the tangential velocity of the moving fingers was below a level of 40 cm/s. This arbitrary level was chosen empirically, since even the fastest grasp on a curved path showed a velocity minimum below this level, and the peak velocity of all movements clearly exceeded this level. Choosing a slightly higher or lower level would not have severely altered the grasping times, since the velocity slopes in this range were very steep due to an acceleration of some 2000 cm/s^2.

The observed grasping time was significantly shorter with visual guidance than for all blind movements. For most subjects, the grasping times under visual control ranged between 50 and 100 ms. Even within such small time windows, this new method of movement recording and analysis permits precise recording without restraining the movement.

Crossman and Goodeve (1983) assumed that visual feedback could aid performance, even within such short periods. They postulated as a precondition that the safe availability of a feedback signal must be foreseeable and no conscious process like a choice reaction of the subject has to be required. They estimated the visual processing time to be as low as 20–50 ms if these conditions were satisfied. The experiments of Zelaznik et al. (1983) showed in a variety of similar paradigms that there were beneficial effects of visual feedback on aiming movements much less than 200 ms. Down to 100 ms the subjects prepared to receive visual feedback when they knew that visual feedback would be available, but they could not use it when it was present but unexpected. These findings are in line with the Permanent Vision Condition data of the present study: the availability of visual feedback produced very short grapsing times.

During the absence of visual feedback in conditions 2–6 a further increase of grasping time was observed, with increasing blind intervals before movement initiation. This fact can be interpreted as a decay of memorized visuo-spatial information. In order to compensate for this hypothesized increasing impairment of short-term memory the subject has to access kinaesthaetic and tactile feedback to a greater extent, resulting in a slowing down of the grasping event. With another experimental approach, Thomson (1983) and Elliott (1986) obtained similar results. In their experiments, subjects walking blindly poduced a deviation from target which was greater the longer they had to wait without vision before starting. In addition, Thomson (1983) reported a sudden increase in errors when a critical interval without vision (some 8 s) was exceeded. This finding was interpreted as the maximum duration that accessible location information was stored in short-term memory. Beyond that time the only spatial information would consist of coded motor programs which could not be adapted to a changed environment. Elliott (1986) was not able to replicate this latter finding. The present study also did not specify a critical time after which the short-term visuo-spatial memory had totally faded.

An interesting feature was seen when conditions 3–5 were compared with conditions 6–8. Although an extended delay without sight of 20 s and above caused a further increase in grasping time, this was not seen with respect to shorter intervals between 5 and 15 s. Perhaps this finding indicates that short-term visuo-spatial memory fades away more rapidly beyond 15 s. Furthermore, the subjects may become aware of the increasing insufficiency of the visuo-spatial memory, a fact that could alter the movement performance. In such cases, a superposition of two mechanisms may result in an increase in grasping time.

During the ongoing experiment, the subjects could have developed an altered strategy to improve performance. One possible strategy could be an attempt to perform the entire prehensive movement more accurately, since the subjects realized that they sometimes missed the target particularly with their eyes closed. A greater accuracy would possibly require a longer movement time if the other parameters were maintained. This dependency was first described by Fitts (1954) and was proved in a variety of subsequent experiments. Such a strategy could simulate the observed effect of longer grasping times in the trials with longer blind delays. Another source of altered grasping time could be induced by increasing practice during the experiment. Such an effect of skill would decrease the impact of visuo-spatial memory in the trials towards the end of the recording session.

The analysis of variance, however, showed that the function of grasping time was not influenced by the number of previously executed trials. Apart from this fact, a certain effect of practice could be observed, which shortened the total movement time with increased skill. Mainly the decreased duration of the high-velocity phases of reaching was responsible for this effect of skill. On the other hand, these high-velocity phases, which served as a measure of the overall speed of performance, were not affected by the visual conditions.

Thus, the behaviour of the grasping time depending on the time of restricted vision cannot sufficiently be explained by any altered mode of performance. Neither a conscious strategy involving the change of parameters such as movement speed nor an effect of skill can be responsible for the present findings. The hypothesis of a short-term memory representing actual visuo-spatial information for a restricted amount of time is in line with the results of the present experiment. As for the main questions about the dynamics and the utilization of such a target-oriented "motor" memory, the results lead to three conclusions. Firstly, the visuo-spatial memory is not able to replace completely a continuous visual feedback during very quick aimed movements with a duration below 100 ms. Secondly, the deprivation of visual information about the target up to approximately 15 s causes prolonged grasping times of 100–150 ms, and grasping is still assisted by a memorized visuo-spatial signal. Thirdly, when the visual deprivation is prolonged beyond 15 s, the target acquisition phase of the aimed movement is additionally delayed, probably because the fading of short-term memory exceeds a critical value.

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