How efficient are central mechanisms for the learning and retention of coincident timing actions?

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Abstract

We compared the adaptive strategy and retention capacity of a deafferented subject and control subjects when intercepting, with a sliding-throw, an apparent movement coming at various speeds. Subjects were submitted to five practice sessions (30 trials per session) and to a retention test. The throwing kinematics was analysed, and spatial and temporal performance errors were measured. With practice, the deafferented subject showed modifications in movement initiation strategies and throwing patterns. With a slow apparent movement, the deafferented subject's initial behavior was characterized by short movement initiation and movement times. With practice, she showed an important increase in movement time in session 5, allowing longer visual control and leading to better temporal and spatial accuracy than that shown in session 1. In the retention session, the deafferented patient showed a late movement initiation strategy, similar to that of the control subjects. This increased movement initiation time was accompanied by an improved temporal accuracy compared to the deafferented subject's early results. However, spatial accuracy improvement was labile and could not be maintained over the retention interval. At the fast speed, all temporal components of the response, namely, movement initiation time (MIT), movement time (MT), and disk travel time (DTT), were similar for the deafferented and control subjects. Overall, the deafferented subject reduced her temporal error through practice, though without attaining the control subjects' accuracy. However, with a fast-moving stimulus, she showed a deteriorated spatial accuracy, even doubling her spatial errors at retention. In brief, the deafferented subject achieved proper temporal (perceptivo-cognitive) lasting control of her interceptive action, whereas spatial (sensorimotor) regulation raised mnemonic problems. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Deafferentation; Proprioception; Coincident timing; Learning; Retention

1. Introduction

In a behavioral system combining central and peripheral elements, one of the first questions to examine is how sensory input is combined with central control [10]. The combined system is acknowledged to have three functions: influence the decision to perform an action, participate in adjusting movement parameters, and, finally, ensure that movements are carried out correctly, despite potential disturbances. The central mechanisms, which operate independently of sensory information, have been shown to play a role in the control of human movements [29]. Are these mechanisms sufficient for the learning and retention of coincident-timing actions? Motor tasks, taking place in a dynamic environment, constitute a system in which the integration of visual and proprioceptive sensory information is both necessary and likely to be supported by internal references whenever movement is too fast to allow on-line feedback control. These timing interceptive behaviors introduce interesting motor learning issues since they also require both a perceptual and a sensorimotor component. Two temporal components are involved, one is related to sensory receptors whereas the other refers to muscular effectors. The perceptual component involves the evaluation of the time required by an object to reach a point of contact, based on the speed of the object and the distance to be covered (receptor anticipation). The sensorimotor component involves a decision about and the moment to initiate an action, based on the knowledge of movement time allowing interception (effector anticipation). Performance accuracy in a coincident-timing task greatly depends on the cognitive strategies used by the subjects, e.g. (a) their decision to release, or to postpone the release, of the intercepting object, and (b) their capacity to modulate the duration and direction of their motor response.
Schmidt [27] has observed strategies used by subjects moving their arm to intercept an apparent movement, and reported very low correlation between temporal error and movement time. Moderate correlations were noted between temporal error and movement initiation time, and between initiation time and movement time. The most accurate subjects maintained a constant movement time and varied their triggering time. The strategies used by the learners were based on past experiences with the task, and on the understanding of task requirements.

In addition, sensory sources of information (either visual or proprioceptive) are the necessary substrates for the establishment of the memory trace that emerges from practice, i.e. from the repetition of a motor activity [4, 10, 11, 20, 21, 197]. This can be illustrated from a series of separate experiments [3, 7, 9], jointly reported in 1995 by Cordo et al. [8]. In these experiments, the authors eliminated visual information and used a throwing-like elbow extension movement, followed by hand opening, synchronized with the elbow reaching of a prescribed angle. The arrival time of the elbow at the target angle was randomly varied, leaving proprioception as the only source of information about the kinematics of the elbow rotation. Overall, they showed that (a) proprioceptive coding of dynamic position can be used by the nervous system to coordinate discrete movement sequences; (b) this proprioceptive processing mechanism was found to be readily available on the first attempts of a novel motor task.

The deafferentation model offers a unique opportunity to further specify the relative contribution of visual and proprioceptive afferents and the differential power of the memory trace established with and without proprioception. We have observed [2, 5, 24], that through vision, a deafferented subject (GL) compensates successfully for her lack of proprioception when pointing to fixed targets. This was also observed with other deafferented subjects [18, 25, 26]. Could the compensatory strategies adopted by subjects, devoid of proprioception, be transferred to a coincidence-anticipation task involving a moving target?

Likewise, we have shown that GL can efficiently learn to produce short timed responses. The temporal accuracy of these responses was maintained over a retention interval and without any knowledge of results [13]. Such findings suggest that, even without proprioceptive information, the cognitive processes involved in the timing aspect of the coincident-timing task could also insure correct temporal regulation of a discrete coincidence-anticipation task.

The aim of the present study was thus to verify the capacity of a subject devoid of proprioception to (a) learn a coincidence-anticipation task, interfacing both a perceptual and a motor aspect and (b) retain improvement after a retention interval.

2. Methods

2.1. Subjects

A female deafferented subject (GL) aged 47 years, and four female control subjects (mean age = 27.6 years') who were unaware of the purpose of the experiment, participated voluntarily, after providing informed consent. The patient suffers from a permanent and specific loss of the large sensory myelinated fibers in the four limbs following two episodes of sensory polyneuropathy, which has affected her whole body below the nose. The illness resulted in a total loss of the senses of touch, vibration, pressure, and kinesthesia, as well as the total absence of tendon reflexes in the four limbs. Motor nerve conduction velocities and the results of a needle electromyography (EMG) investigation of the muscles of the arm are normal [6]. These observations have been confirmed and have proven stable for the past 18 years. Though the patient is confined to a wheelchair, she does most of the daily manual work at home under constant visual guidance (cf. [6] for a more complete clinical description of the patient).

2.2. Task and apparatus (Fig. 1)

The coincidence-anticipation task consisted in intercepting an apparent movement with the sliding-throw of a plastic disk on a table (210 cm long x 105 cm high). The apparent movement of the stimulus was created by the successive lighting of 44 light emitting diodes (LEDs) 5 cm apart, placed at the end of the table on the subject's left hemifield. The target was the last LED (i.e. diode 44), which was clearly identified by a white circle. Subjects were seated facing the table at waist height. Throwing accuracy was detected through photocells, 1 cm apart, distributed at the end of the table under the electroluminescent diodes creating the apparent movement. The distance between the photocells allowed spatial measurement with a 0.5 cm accuracy.

A SELSPOT 3-camera motion analyser system was used to record the kinematics of the throwing by means of an electroluminescent diode, fixed on the subject's wrist. Filtered position and velocity-time profiles were obtained from optimally regularized Fourier series [16].

2.3. Design and protocol

Two stimulus speeds were used: 125 and 200 cm/s (hereafter called slow and fast speeds, respectively). The distance covered by the stimuli was 220 cm, which yielded a stimulus exposure duration of

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1Fleury et al. [12] have shown that normal adult subjects aged 45-52 years learned and performed the same coincident-timing task as well as young adults.
Fig. 1. Experimental setup. Subjects intercepted an apparent movement with the sliding-throw of a plastic disk down a table.

17,600 ms for the slow and 11,000 ms for the fast speed. Subjects were submitted to five practice sessions and a final retention session. Each session consisted of 15 trials at each speed, which were randomly presented within a bloc of 30 trials. Kinematic measures were collected for practice sessions 1 and 5 and for the retention session.

For the 10 familiarization trials, before the first session only, subjects received quantified knowledge of the results of their spatial (in cm) and temporal accuracy (in ms). Subjects were then submitted to six sessions (1-5 and retention). During these sessions, subjects performed the task without quantified knowledge of results, but could always make a visual evaluation of their throwing accuracy. They also always had vision of their throwing hand. On the first day, subjects were submitted to familiarization trials and performed sessions 1 and 2 in the morning and sessions 3-5 in the afternoon. A 5 min rest period separated concomitant sessions. To examine retention effect, subjects performed another session three days later.

2.4. Dependent variables

The following measures were used: (a) the absolute temporal error, i.e. the temporal delay between the arrivals of the disk and the stimulus on the target, (b) the absolute spatial error, i.e. the distance between the disk’s impact point and the target, (c) movement initiation time, i.e. the delay between the onset of the apparent movement and the triggering of subject’s movement (MIT), (d) movement time (MT), i.e. the time elapsed between the triggering of the movement and the disk release. Moreover, peak velocity (PV) and time to peak velocity (TPV) were obtained from hand movement.

To compare the results of the patient and control subjects, six t-tests of the comparison of a single observation with the mean of a sample (3 sessions and 2 speeds) were applied to all dependent measures. Moreover, within-subject comparisons were applied to investigate modifications through practice and were reported whenever both an analysis of variance and a t-tests proved them significant with a probability of 0.05. Learning is considered here to be a relatively stable improvement in the subjects’ performance reflected in the reduction of subjects’ temporal and/or spatial errors and variability, from the first session to the retention test performed after a temporal delay following the last practice session [23, 30]. Operationally, an improvement is considered to be a within-subject accuracy or stability that is progressive and significantly higher than that obtained in the first session, for at least two sessions including, of course, the retention session.
3. Results

3.1. Interceptive patterns strategies

With practice and at the slow speed, the deafferented subject showed significant modifications in movement initiation strategies and throwing patterns. This behavior is illustrated in Fig. 2. Indeed two initiation patterns strategies can be observed. When comparing session 1 and session 5, movement initiation time was kept relatively constant, while movement time increased (298 vs 553 ms). When comparing session 1 and the retention session, movement initiation time increased (649 vs 1016 ms), while movement time decreased (298 vs 199 ms). These two initiation patterns strategies allowed GL to decrease her temporal error (320, 179 and 122 ms for sessions 1, 5, and the retention session, respectively—cf. Fig. 3). The delayed movement initiation strategy adopted by GL at retention was similar to that observed for controls in all sessions. Despite an improvement in temporal accuracy at retention, GL still showed greater temporal errors than the controls (122 ms vs 74 ms). At the fast speed, all the temporal components of the response, namely movement initiation time, and movement and disk travel times, were similar for GL and the controls.

Across stimulus speeds, GL's and controls' movement initiation strategies were quite different. For session 1, GL's movement initiation patterns were little differentiated in relation to speed (649 and 466 ms for slow and fast speed stimuli, respectively). Conversely, in the control subjects, movement initiation times were 1071 and 471 ms for the slow and fast speeds, respectively, emphasizing the importance of coding speed when programming interceptive responses. The control subjects kept their motor response constant, supported by proprioceptive control, and modified their movement initiation according to stimulus speed. With practice, GL's motor response was also modified as a function of stimulus constraint, but only at retention does a more constant motor pattern appear. However, spatial

Fig. 2. Temporal behavior for practice sessions and retention for GL and controls. With practice and at the slow speed, GL showed significant modifications in movement initiation delays and throwing patterns, whereas the controls maintained very stable movement initiation and movement times. GL = the deafferented patient; SI = practice session 1; S5 = practice session 5; R = retention.
accuracy results revealed that the movement was not yet efficient.

### 3.2. Temporal and spatial errors

Overall, GL gradually reduced her temporal errors through practice 2, although she did not attain the controls’ accuracy (cf. Fig. 3 and Table 1). Indeed, all the controls performed accurately in space and time after only a few practice trials. At retention, GL’s increase in movement initiation time (MIT), although improving temporal accuracy, yielded increased spatial errors 3.

In terms of spatial performance, the control subjects showed remarkable spatial constancy at both speeds throughout all practice sessions, their spatial error ranging from 4.5-5.5 cm only. However, spatial accuracy raised a major problem for GL. Her spatial error was from 2-4 times that of the controls, at both stimulus speeds. At the slow speed, the improvement shown after practice was not completely maintained at retention, once again resulting in less accurate movements than those of the controls. At the fast speed, GL showed progressively increasing spatial errors with practice, even doubling her initial errors.

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2 From practice session 2 (238 ms) to practice session 3 (109 ms), GL improved her temporal accuracy significantly and maintained this improvement in practice session 4 (118 ms).

3 From practice session 2 (11 cm) to practice session 3 (14 cm), GL’s spatial accuracy deteriorated and remained the same (14 cm) in practice session 4.

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Table 1

<table>
<thead>
<tr>
<th>Subject</th>
<th>SIS</th>
<th>S1F</th>
<th>S5S</th>
<th>S5F</th>
<th>RS</th>
<th>RF</th>
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<tr>
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<td>27.32</td>
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<td>44.63</td>
<td>46.50</td>
<td>46.23</td>
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<tr>
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<td>32.35</td>
<td>44.02</td>
<td>27.36</td>
<td>39.99</td>
<td>27.53</td>
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<tr>
<td>Control 3</td>
<td>97.32</td>
<td>67.98</td>
<td>29.46</td>
<td>34.64</td>
<td>20.21</td>
<td>14.29</td>
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<tr>
<td>Control 4</td>
<td>98.78</td>
<td>21.22</td>
<td>34.64</td>
<td>29.10</td>
<td>42.95</td>
<td>38.98</td>
</tr>
<tr>
<td>GL</td>
<td>180.77</td>
<td>89.29</td>
<td>118.60</td>
<td>67.71</td>
<td>112.43</td>
<td>57.29</td>
</tr>
</tbody>
</table>

SIS = practice session 1 at slow speed; S1F = practice session 1 at fast speed; S5S = practice session 5 at slow speed; S5F = practice session 5 at fast speed; RS = retention session at slow speed; RF = retention session at fast speed.
at retention. Though she was able to improve her temporal accuracy, this occurred at the expense of spatial accuracy.

3.3. Movement kinematics

The comparative analysis of GL’s and the controls’ maximal velocity and time to peak velocity did not reveal differences except for session 5 at the slow speed. During this session, GL significantly decreased both her maximal velocity (2742 mm/s vs 573 mm/s at session 1 and 5, respectively) and time to peak velocity (267 ms vs 516 ms for sessions 1 and 5, respectively) compared to the controls (maximal velocity = 1959 mm/s vs 1907 mm/s for sessions 1 and 5, respectively; time to peak velocity = 250 ms vs 233 ms for sessions 1 and 5, respectively). The latter result emphasized GL’s search for a new strategy, i.e. increasing her movement time in order to lengthen her visual guidance of the disk, which lead to better spatial accuracy. Figure 4 shows that at the slow speed, while control subjects present constant maximal and time to peak velocities, for both measures, GL presented significantly modified patterns from sessions 1-5 and from session 5 to retention (Ps — 0.01).

4. Discussion and conclusion

Overall, with a fast-moving stimulus, GL’s interceptive temporal components were similar to that of the controls. Indeed, motor and not sensory representation has proven to be the major determinant of rapid aiming movements [1]. GL’s performance at the fast speed supports the separation of sensory (recognition) and motor (production) representations suggested by Bailey and further advocated by Schmidt [28]. Despite her temporal performance, at the fast speed, GL’s spatial accuracy is inferior to that of the controls. This is not surprising, considering that the time available (~ 1 s) to (a) make a decision to release or postpone the release of the intercepting disk and/or (b) modulate the accuracy of the throwing response, is limited. The slow speed condition, less time restrictive (~1.7 s), is more liable to yield between-subject differences. Indeed it uncovered two different strategies used by the deafferented subject to successfully intercept the moving stimulus. (1) In practice session 5, GL exhibited an on-line visual control of the throwing response, lengthening her movement time and increasing both her temporal and spatial accuracy. (2) At retention, her movement initiation time was modulated according to speed, and

![Fig. 4. Representative velocity curves according to Practice Session with a slow-moving stimulus. Vertical lines represent the moment of disk release, which corresponds to time to peak velocity. At the slow speed, while the controls showed constant maximal and time to peak velocities, for both measures, GL presented significantly modified patterns from sessions 1-5 and from session 5 to retention.](image-url)
temporal accuracy was still improving. Nevertheless, her shorter movement time again resulted in a deterioration of spatial accuracy. This suggests that the efficient storing of interceptive location is enhanced by the presence of proprioception, even in short discrete and ballistic types of movements such as interceptions. Figure 2 shows that the hand movement in control subjects lasted less than 300 ms. Similar results were observed for GL, except when she adopted a visual control strategy in session 5 (slow speed). Figure 4 shows that movements were indeed ballistic and that the disk release always occurred at or very close to the peak hand velocity. It is worth noting that GL, when using an increased movement time in session 5, reached a spatial accuracy comparable to that of the controls. When she adopted a new strategy at retention, i.e. increasing her movement initiation time, she produced a ballistic movement very similar to that of the controls. Nevertheless, having lost part of the visual support yielded by the increased visual guidance of the disk, which was characteristic of her behavior in session 5, she came back to a spatially erratic behavior. This suggests that a throwing movement, although very short, depends on the contribution of proprioception to establish a stable mnemonic trace in controls.

While direct proprioceptive coding of joint rotation is immediately available to co-ordinate discrete actions in controls, as suggested by Cordo [7], in the absence of proprioception, position information processed through vision seems to require a more intensive and time-consuming learning process, at least in the task of intercepting a moving stimulus.

The finding that GL maintained an improvement in temporal accuracy over a retention delay, suggests that temporal control, of a cognitive-perceptual nature, is within reach of a deafferented subject, whereas spatial control, a more sensorimotor form of control, creates serious mnemonic problems.

In session 1, GL’s less differentiated movement initiation delays were relatively similar whatever the stimulus speed, compared to that of the controls, which differentiated. This suggests the involvement of proprioception in the establishment of an interface perception/action, enabling the control subjects to show immediate adaptation to the stimulus characteristics. Considering the difficulty involved in the execution of accurate movements in space, GL’s preferred strategy was to produce a constant movement preparation, whatever the stimulus speed. With a fast-moving stimulus, her movement initiation time approached a simple reaction time, which allowed her to produce a response close to that of the controls. Conversely, at the slow speed, using the same motor pattern led her to trigger her movement too soon, thus yielding an important temporal error. Such undifferentiated initial patterns were also observed in a previous weight discrimination study whereby objects of the same shape, but of different weights, were lifted by GL with a constant pulse [142]. Proprioception would, therefore, be a contributor to the plasticity exhibited by the controls when facing alterations in stimulus characteristics.

With practice, the deafferented subject learned to control the temporal but not the spatial aspect of an anticipation-coincidence task, especially at the slow speed. This finding supports previous results on GL’s ability to estimate and produce temporal duration correctly [13]. The temporal or cognitive-perceptual aspect of the interceptive behavior emerges as being more likely to improve with practice than the sensorimotor (spatial) aspect, where a proprioceptive support seems essential for the establishment of a durable memory trace for the motoric aspect of the task. The efficiency of visual-kinesthetic information in ‘reading’ lifting movements while judging weights does not seem to be transferable to time-to-contact judgments, wherein cognition is involved in goal-reaching in space rather than mere discrimination.

Our results support the fact that the absence of proprioception: (a) renders difficult the performance of an interceptive task; (b) necessitates an adaptation or learning period for the reaching of temporal accuracy; and (c) does not allow the establishment of a durable spatial mnemonic trace for interceptive responses. In brief, in the present study, the deafferented subject reached proper temporal (perceptive-cognitive) lasting control of her interceptive action, whereas spatial (sensorimotor) regulation raised mnemonic problems.

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