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Sensorimotor adaptation to violations of temporal contiguity

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Abstract. Most events are processed by a number of neural pathways. These pathways often differ considerably in processing speed. Thus, coherent perception requires some form of synchronization mechanism. Moreover, this mechanism must be flexible, since neural processing speed changes over the life of an organism. Here we provide behavioral evidence that humans can adapt to a new intersensory temporal relationship (which was artificially produced by delaying visual feedback). The conflict between these results and previous work that failed to find such improvements can be explained by considering the present results as a form of sensorimotor adaption.

1 Introduction

Even though the different sensory modalities process information from a common event at different speeds, our perceptual experience of the world is neither fragmentary nor disjointed. This lack of fragmentation is even more surprising given that different neural pathways within a modality often differ in processing speed (Bolz, Rosner, & Wässle, 1982; Sestokas & Lehmkuhle, 1986) and that the response latency of neurons within a pathway can vary even to identical stimuli (Sestokas & Lehmkuhle, 1986; Shapley & Victor, 1978). These facts strongly suggest that the human brain is able to synchronize the different modalities and neural pathways by compensating for variations in neural processing time, and several models of such a mechanism have been proposed (Baldi & Meir, 1990; Eckhorn, Reitboeck, Arndt, & Dicke, 1989; Grossberg & Grunewald, 1997; König & Schillen, 1991).

Neural architecture changes over the lifetime of an organism in general and experience can alter the mean cortical response latency to preferred stimuli in particular (Ahissar & Ahissar, 1994). It would seem, then, that any synchronization mechanism would need to be flexible in order to properly perform its function. Yet, previous research found little or no behavioral evidence that the human visuo-motor system can adapt to changes in intersensory temporal relationships (Sheridan & Ferrel, 1963; Smith, Mc-Crary, & Smith, 1962; Smith, Wargo, Jones, & Smith, 1963). Indeed, this consistent failure has lead some to claim that humans cannot, even in principle adjust to such changes (Smith, McCrary, & Smith, 1962). Here we provide behavioral evidence that humans can and do adapt to such changes.

The experiments reported here build explicitly upon the early prism adaptation work, where the visual field was usually shifted laterally by wearing prism goggles, resulting in an intersensory discrepancy about the location of objects (for a review, see Bedford, 1993). Since each object can have only one spatial location, any intersensory disagreement about this location may be considered a miscalibration or misalignment of the sensory systems. Subsequent training with the discrepancy leads to visuo-motor adaptation or 'recalibration'.

Following the same logic, one might suggest that since any single part of an event can occur at only one point in time, any intersensory temporal offset might be taken as evidence of a temporal miscalibration (i.e., de-synchronization). Here we test for adaptation to intersensory temporal offsets using an obstacle avoidance task with the visual feedback delayed by 235 ms.

2 Methods

2.1 Displays:

After informed consent was obtained from the subjects, they were seated approximately 50 cm from a computer monitor, and asked to maneuver a small (0.2 cm) white airplane through a dense field of obstacles (see Figure 1). They moved

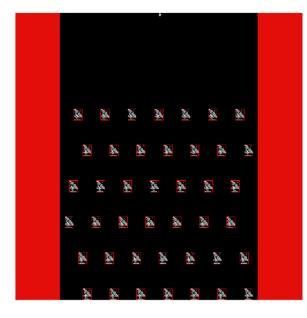


Figure 1: A snapshot of the display. The plane (top of the display) descends at a constant speed through the obstacle field.

the plane via an isometric mouse (i.e., the horizontal motions of the mouse were duplicated exactly at a scale of 1:1 on the computer monitor). The plane traveled at one of ten fixed vertical speeds (2.9, 3.2, 3.5, 3.9, 4.4, 5.0, 5.9, 7.1, 8.8, and 11.8 cm/s.). Each obstacle (0.7 cm) depicted a gray and white radar dish enclosed in the outline of a red square. The obstacle field (12.5 cm high by 17 cm wide) consisted of forty-two obstacles placed in a jittered lattice-work pattern (6 rows. 7 columns). The lattice-work was arranged so that (a) no straight, vertical path through the field existed and (b) obstacles were vertically and horizontally separated by 1.4 cm. The field was flanked by two large, red rectangles (each 19.5 by 4 cm).

2.2 Experimental Group:

Each trial consisted of a single pass through the obstacle field, and was terminated immediately after the subject either successfully traversed the field or collided with an obstacle or red flanking region. Written feedback as well as the visual consequences were presented for each collision or success. The plane's speed was demonstrated prior to each trial in the Pre- and Posttest.

The session was divided into three sections: Pretest, Training, and Posttest. In the Pre- and Posttests, the plane lagged behind the mouse by approximately 35 ms. Since this delay is the smallest of which the computer was capable, and was not noticeable, it is referred to as the "immediate feedback" condition. In Pretest, each speed was presented 5 times, in random order. For each subject, the fastest speed successfully completed on at least 4 of the 5 repetitions in the Pretest was recorded as their "Top Speed". In the Training section, visual feedback was delayed by an additional 200 ms. To gradually increase the difficulty of the training, the speeds were presented from slowest to fastest. If a subject succeeded on 8 of 10 consecutive trials, they were presented with the next faster speed. If they collided 10 times in a row, training ended and the posttest began. If neither occurred within 70 trials, training ended and posttesting began. During the Posttest, the temporal relationship between the plane and the mouse is necessarily perceivable, which might cause subjects to re-adapt to the immediate condition. Thus, the Posttest consisted of only 10 trials, all at the subject's Top Speed.

2.3 Control group:

The control group's session was identical to the experimental group's, with the exception that the control group's Training section was replaced with a similar amount of time watching a movie.

3 Results

Subjects did not perform well at the start of training. Indeed, most subjects complained that the delay seemed extremely large and doubted whether they could perform the task under such conditions. As training progressed, however, subjects were able to traverse the obstacle field more easily and they ceased to complain about the delay. Towards the end of training, most subjects were able to navigate the obstacle field at roughly the same speed with a delay as without one (as measured by their Pretest performance: 6.0 cm/s, on average). This increase in performance as a function of training contrasts remarkably with untrained subjects' performance (3.9 cm/s with delayed feedback). Additionally, towards the end of training, several subjects spontaneously reported that the visual and haptic feedback seemed simultaneous, despite the fact that there was still a 235 ms offset. This suggests that training also changed the perceptual relationship between the two sensory modalities.

The most common measurement of the strength of adaptation is the size of its "negative

aftereffect". That is, adaptation to the intersensory discrepancy reduces a subjects ability to accurately perform the task without the discrepancy (as determined by comparing Post- and Pretest performance). In the present experiment, a strong negative aftereffect was found for every subject in the experimental group (see Table 1). On average, subjects were able to successfully traverse the field on 84% of the trials at their Top Speed in the Pretest, but on only 32% of the trials in the Posttest (a 52% drop from Pre- to Posttest, both of which had immediate feedback). In contrast, performance change for subjects in the control group is largely negligible (7% drop, on average; see Table 2). A two tailed t-test revealed the difference between the two groups to be statistically significant (t(18) = -5.53, p < 0.0001).

Table 1: Experimental group. The score is the percentage of the 10 Posttest trials where the subject successfully navigated the obstacle field.

Subject	Top Speed	Pretest	Posttest
1	5.9 cm/s	100%	20%
2	5.9 cm/s	80%	30%
3	5.9 cm/s	80%	50%
4	5.0 cm/s	80%	20%
5	5.9 cm/s	80%	40%
6	8.8 cm/s	80%	0%
7	7.1 cm/s	80%	10%
8	3.5 cm/s	80%	60%
9	5.0 cm/s	100%	50%
10	7.1 cm/s	80%	40%
average	6.0 cm/s	84%	32%

Table	2:	Control	Group.
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Subject	Top Speed	Pretest	Posttest
1	3.9 cm/s	80%	90%
2	3.9 cm/s	80%	90%
3	7.1 cm/s	80%	80%
4	2.9cm/s	100%	90%
5	5.0 cm/s	80%	90%
6	4.4 cm/s	100%	100%
7	5.9 cm/s	100%	80 %
8	5.0 cm/s	100%	70%
9	5.9 cm/s	100%	90%
10	3.2 cm/s	100%	70%
average	4.7 cm/s	92%	85%

4 Discussion

These results demonstrate quite clearly that humans can learn to perform complex tasks with delayed feedback. Is this improvement the result of sensorimotor adaptation? In his classic book, Welch (1978) defines adaptation to perceptual rearrangements as, "a semipermanent change of perception or perceptual motor coordination that serves to reduce or eliminate a registered discrepancy between or within sensory modalities or the errors in behavior induced by this discrepancy" (p.8). The above results certainly demonstrate a change in perceptual motor behavior that nearly eliminated errors caused by an intersensory perceptual rearrangement, and they suggest that there was a perceptual change as well.

In addition to meeting Welch's definition of adaptation, the pattern of results is strikingly similar to that found with prism adaptation. Specifically, (a) an intersensory discrepancy impairs performance at first; (b) a few minutes of exposure to the consequences of the offset returns performance accuracy and speed to normal ranges; (c) practice without being exposed to the consequences of a delay (i.e., by allowing subjects to slow down) does not lead to improved performance; (d) the training produces a strong negative aftereffect; (d) the training also seems to result in a change in the perceived relationship between the two sensory modalities.

The robust nature of the present results makes the consistent failure of previous research to find improvement with practice somewhat surprising. One possible explanation for this apparent conflict might be provided by the parallel with prism adaptation. This parallel has two points of critical importance. First, time like space is a physically and perceptually continuous dimension (Gibson, 1979), and temporal perception is not limited to simple binary judgments (e.g., "now" versus "before"). Second, and perhaps more critical is the fact that sensorimotor adaptation requires that the subjects be exposed to the consequences of the discrepancy (to use Welch's terminology, the discrepancy needs to be either consciously or unconsciously "registered"). It has been established that humans tend to slow down when presented with delayed feedback (Sheridan & Ferrel, 1963) – a strategy that negates the effects of the delay. For example, a driver traveling 36 km/h in a car with a 1 s delay must turn the steering wheel 10 meters prior to reaching an intersection. Traveling at 3.6 km/h, however, they need to turn only 1 meter early - the effects of the delay are strongly mitigated and the driver can turn once in the intersection. Since the subjects in the early work on practice with temporal offsets decreased their

speed, and thus were not exposed to the consequences of the perceptual rearrangement, it is not surprising that no adaptation to the offsets was found.

While adaptation to temporal offsets strongly parallels prism adaptation, it is not clear that the two are formally similar let alone use a similar mechanism. It is certain, however, that the present results must be due to some form of unconscious learning. If the improvement was due solely to a conscious strategy (e.g., simply trying to "turn early" or "anticipate" the turns), then the removal of the delay should have lead the subjects to change their strategy (Bedford, 1993; Welch, 1978) and there would have been no negative aftereffect. This point is made more salient by two facts. First, just before starting the Posttest, subjects were informed that the Posttest used immediate feedback just as the Pretest did. Second, during the Posttest, subjects were able to directly experience the immediacy of the feedback. Even with these reminders to change strategies, subjects were still unable to complete the task for most of the Posttest.

An explanation based on motoric memorization (e.g., using the same pattern of muscle innervations) or overtraining likewise cannot explain the results. While most subjects used the same path throughout the experiment, the changes in speed considerably altered the duration and temporal spacing of maneuvers¹. This makes overtraining unlikely, particularly with only 10 to 40 trials, on average, per speed. A more persuasive argument against explanations based on motoric memorization is the fact that final speed seen in the Training section was, for a number of subjects, the same speed seen in the Posttest. In such cases, the only difference between the end of training and the Posttest was the size of the temporal offset between visual and haptic feedback. The exact same motor patterns that are successful at a speed of 7.1 cm/s with 235 ms delay will be successful at a speed of 7.1 cm/s with no delay. For these subjects, at least, any difference in performance between the two types of trial **must** be attributed to some change in the visuo-motor relationship.

Finally, and perhaps most critically, the conditions used by all of the previous work on practice with delayed feedback are just as appropriate for behavioral strategies, overtraining, and motor memorization as the conditions reported here, yet none of the previous work found improvement in performance.

In summary, the present results clearly demonstrate that, with the proper experience, the internal delay inherent in intersensory integration can be altered. This alteration is a form of unconscious learning, with the pattern of results being consistent with sensorimotor adaptation.

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¹The task required a rather high precision in both space and time. For example, at a speed 7.1 cm/s, subjects had to maneuver through 6 rows of obstacles within 1.75 seconds with a cumulative error (even very small errors on the first turn drastically affects the position for all subsequent turns). The precision required for some of these maneuvers is less than 1 cm and 100 ms.

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