

Research Report

SENSORIMOTOR ADAPTATION TO VIOLATIONS OF TEMPORAL CONTIGUITY

Douglas W. Cunningham,^{1,2} Vincent A. Billock,² and Brian H. Tsou³

¹Max Planck Institute for Biological Cybernetics, Tübingen, Germany; ²Logicon Technical Services; and ³U.S. Air Force Research Laboratory, Human Engineering Division, Crew Systems Integration Branch

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, because 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 adaptation.

Even though the different sensory modalities process information from a common event at different speeds, people's 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 neurons within a pathway can have varying response latencies 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 seems, 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 (Held, Efsthathiou, & Greene, 1966; Sheridan & Ferrel, 1963; K.U. Smith, Wargo, Jones, & Smith, 1963; W.M. Smith, McCrary, & Smith, 1962). Indeed, this consistent failure has led some researchers to claim that humans cannot, even in principle, adjust to such changes (K.U. Smith et al., 1963). 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, in which the visual field was usually shifted laterally by prism goggles, resulting in an intersensory discrepancy about the location of objects (for reviews, see Bedford, 1993; Welch, 1978). Given that 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 (Bedford, 1999). Subsequent training with the discrepancy leads to visuo-motor adaptation, or "recalibration."

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

METHOD

Subjects

Twenty paid, naive subjects participated in the experiment. The subjects were randomly assigned to either the experimental or the control group.

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 Fig. 1). They moved 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 10 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 42 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).

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. As feedback is critical for adaptation to occur, each trial ended with a written message indicating success or failure, as well as the visual consequences of performance. The plane's speed was demonstrated prior to each trial in the pre- and posttests.

The experiment was divided into three phases: pretest, training, and posttest. In the pre- and posttest phases, the plane lagged behind the mouse by approximately 35 ms. Given that this delay is the smallest of which the computer was capable, and was not noticeable, we refer to this as the immediate-feedback condition. In the pretest, each speed was presented five times, in a random order (each speed was seen once

Address correspondence to Douglas W. Cunningham, Max-Planck-Institute for Biological Cybernetics, Spemannstrasse 38, 72076 Tübingen, Germany; e-mail: douglas.cunningham@tuebingen.mpg.de.

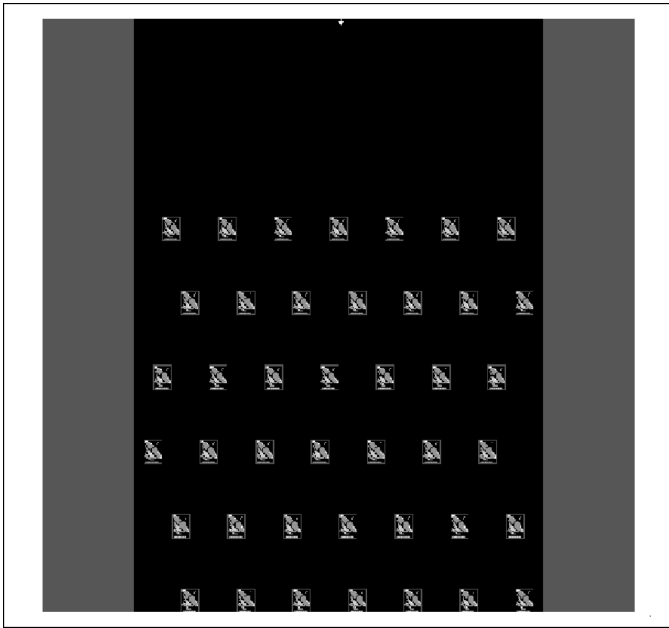


Fig. 1. A snapshot of the display. The plane (which started at the top of the display) descended at a constant vertical speed through the obstacle field.

before any speed was presented a second time). The fastest speed at which each subject successfully traversed the obstacle field on at least four of the five repetitions in the pretest was recorded as that subject's top speed. In the training phase, visual feedback was delayed by an additional 200 ms. In a pilot study, it was found that a 235-ms delay does impair performance on this task (the top speed for untrained subjects was, on average, 6.2 cm/s with no delay but only 3.9 cm/s with a 235-ms delay). To gradually increase the difficulty of the training, we presented the speeds from slowest to fastest. If a subject succeeded on 8 of 10 consecutive trials, he or she was presented with the next faster speed. If the subject collided 10 times in a row, training ended and the posttest began. If neither of these two criteria was met within 70 trials, training ended and the posttest began. During the posttest, the temporal relationship between the plane and the mouse was necessarily perceivable, which might have caused subjects to readapt to the immediate-feedback condition, masking any aftereffect of the training. To minimize the possibility of readaptation, we included only 10 trials, all at the subject's top speed, in the posttest.

Control Group

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

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.

Toward the end of training, most subjects were able to navigate the obstacle field at roughly the same speed with a delay as without one. That is, the top speed in the pretest was, on average, 6.0 cm/s, and the fastest speed during training for which the success criterion was reached was, on average, 6.9 cm/s.

The most common measurement of adaptation is the *negative aftereffect*. That is, adaptation to an intersensory discrepancy reduces a subject's ability to accurately perform the task without the discrepancy (as determined by comparing pre- and posttest 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 at that speed in the posttest (a 52% drop from the pretest phase to the posttest phase, both of which had immediate feedback). In contrast, the change in performance for subjects in the control group was 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, $t(18) = -5.53, p < .0001$.

Finally, several subjects spontaneously reported that, toward the end of training, the visual and proprioceptive feedback seemed simultaneous. Furthermore, when the delay was removed, the plane seemed to move before the mouse did—effect appeared to come before cause. Although these results are anecdotal, they suggest that temporal adaptation alters the intersensory perceptual relationship, and that the corresponding perceptual negative aftereffect is an apparent reversal of causality.

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) defined adaptation to perceptual rearrangements as "a semipermanent change of perception or perceptual motor coordination that

Table 1. Results for the experimental group

| Subject | Top speed (cm/s) | Percentage of trials at top speed completed successfully | |
|---------|------------------|--|----------|
| | | Pretest | Posttest |
| 1 | 5.9 | 100 | 20 |
| 2 | 5.9 | 80 | 30 |
| 3 | 5.9 | 80 | 50 |
| 4 | 5.0 | 80 | 20 |
| 5 | 5.9 | 80 | 40 |
| 6 | 8.8 | 80 | 0 |
| 7 | 7.1 | 80 | 10 |
| 8 | 3.5 | 80 | 60 |
| 9 | 5.0 | 100 | 50 |
| 10 | 7.1 | 80 | 40 |
| Average | 6.0 | 84 | 32 |

Note. The top speed for each subject is the fastest speed at which he or she could successfully navigate the obstacle field at least four times out of five repetitions during the pretest. During the posttest, each subject was presented with 10 trials all at that subject's fastest pretest speed.

Table 2. Results for the control group

| Subject | Top speed (cm/s) | Percentage of trials at top speed completed successfully | |
|---------|------------------|--|----------|
| | | Pretest | Posttest |
| 1 | 3.9 | 80 | 90 |
| 2 | 3.9 | 80 | 90 |
| 3 | 7.1 | 80 | 80 |
| 4 | 2.9 | 100 | 90 |
| 5 | 5.0 | 80 | 90 |
| 6 | 4.4 | 100 | 100 |
| 7 | 5.9 | 100 | 80 |
| 8 | 5.0 | 100 | 70 |
| 9 | 5.9 | 100 | 90 |
| 10 | 3.2 | 100 | 70 |
| Average | 4.7 | 92 | 85 |

Note. The top speed for each subject is the fastest speed at which he or she could successfully navigate the obstacle field at least four times out of five repetitions during the pretest. During the posttest, each subject was presented with 10 trials all at that subject's fastest pretest speed.

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 results of this experiment certainly demonstrate a change in perceptual-motor behavior, and this change nearly eliminated errors caused by an intersensory perceptual rearrangement. The results suggest that there was a perceptual change as well.

In addition to meeting Welch's definition of adaptation, the results show a pattern 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 return performance accuracy and speed to normal ranges; (c) the training produces a strong negative aftereffect; and (d) the training also seems to result in a change in the perceived intersensory relationship.

The robust nature of the present results makes the consistent failure of previous research to find significant improvement with practice somewhat surprising. One possible explanation for this apparent conflict might be provided by a parallel with prism adaptation. First, it is important to note that time is much like space, particularly in the respect that they are both physically and perceptually continuous dimensions (Gibson, 1979) that are processed by several sensory modalities. Thus, it is possible in principle to obtain small, quantitative shifts (i.e., "recalibrations") in the sensorimotor and intersensory relationships (either spatial or temporal). Second, and perhaps more critical, it has been clearly demonstrated that sensorimotor adaptation requires subjects to be exposed to the consequences of the discrepancy (to use Welch's term, the discrepancy needs to be either consciously or unconsciously "registered"). Thus, it is of central importance to note that subjects in previous studies slowed down when the delay was present. Indeed, humans generally tend to decrease their speed when presented with delayed feedback (Sheridan & Ferrel, 1963). This is crucial because slowing down can effectively eliminate the consequences of the delay. For example, a driver traveling at 20 m/s in a car with a 1-s delay must turn the steering wheel 20 m prior to reaching an intersection. Traveling at 2 m/s, however, the driver needs to turn only 2 m early—the effects of the delay are strongly mitigated, and the driver

can turn once in the intersection. It can be argued, then, that subjects in the earlier work were not really exposed to a sensorimotor discrepancy and could not register the discrepancy. Thus, it is not surprising that no adaptation to the delay was found.

The astute reader might have noticed that when there is a fixed intersensory delay for an object that is moving with a constant velocity (both speed and direction), there will be a fixed intersensory spatial offset. For example, when an object travels at 6.0 cm/s straight down with a 235-ms visual delay, its seen position would always be 1.41 cm higher than its felt position. At first blush, it might seem that the present results could be due to adaptation to this spatial offset. However, such an explanation will not work for several reasons. First, the horizontal component of the plane's velocity was not constant: The task required that subjects actively move the plane to the left or right to avoid collisions. Because the horizontal spatial offset changed rapidly, often, and in a nonperiodic manner, an explanation based on spatial adaptation would require that subjects continuously recalibrate to an unpredictably changing offset. This type of spatial adaptation is unknown and unlikely (Welch, 1978). Second, the delay affected the causal relationship of the task: Proprioceptive motions occurred 235 ms before the visual motions they caused. No form of spatial adaptation can compensate for this lag. Finally, it has been shown that delaying visual feedback by 50 ms or more significantly impairs adaptation, with delays greater than 225 ms sometimes totally eliminating spatial adaptation (Hay & Goldsmith, 1973; Held & Durlach, 1993; Held et al., 1966; Kitazawa, Kohno, & Uka, 1995). Thus, the present results cannot be due to spatial adaptation.

Likewise, the results cannot be due solely to a conscious strategy (e.g., simply trying to "turn early" or "anticipate" the turns). The removal of the delay should have led 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 it used immediate feedback. 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 is also insufficient. Although most subjects used the same path throughout the experiment, the changes in speed considerably altered the duration and temporal spacing of maneuvers.¹ This makes overtraining unlikely, particularly with only 10 to 40 trials per speed, on average. Furthermore, the final speed seen in the training phase 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 proprioceptive feedback. The exact same motor patterns that are successful at a speed of 7.1 cm/s with a 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.

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

Finally, and perhaps most critically, the primary methodological change in the present work was to force subjects to drive at an externally chosen speed. There is nothing about this change from prior studies that makes the use of strategies more likely. Likewise, there is nothing that would differentially encourage overtraining or motoric memorization. This, combined with the fact that previous work found little improvement in performance, strongly suggests that the present results are not due to conscious strategies, overtraining, or motoric memorization. Indeed, because the method did differentially encourage sensorimotor adaptation, it seems logical that the improvement stemmed, at least in part, from such adaptation.

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, and the pattern of results is consistent with an explanation based on sensorimotor adaptation. The results also suggest that temporal adaptation can alter the perception of simultaneity, and possibly reverse the perception of causality.

Acknowledgments—We would like to thank Felice Bedford, Ian Thornton, Markus von der Heyde, Astros Chatziastros, Bernhard Riecke, and Isabelle Berndt for fruitful discussions and comments on an earlier draft of this manuscript.

REFERENCES

- Ahissar, E., & Ahissar, M. (1994). Plasticity in auditory cortical circuitry. *Current Opinion in Neurobiology*, 4, 580–587.
- Baldi, P., & Meir, R. (1990). Computing with arrays of coupled oscillators: An application to preattentive texture discrimination. *Neural Computation*, 2, 458–471.
- Bedford, F.L. (1993). Perceptual learning. *The Psychology of Learning and Motivation*, 30, 1–60.
- Bedford, F.L. (1999). Keeping perception accurate. *Trends in Cognitive Sciences*, 3, 4–11.
- Bolz, J., Rosner, G., & Wässle, H. (1982). Response latency of brisk-sustained X and brisk-sustained Y cells in the cat retina. *Journal of Physiology (London)*, 328, 171–190.
- Eckhorn, R., Reitboeck, H.J., Arndt, M., & Dicke, P. (1989). A neural network for feature linking via synchronous activity. In R.M.J. Cotterill (Ed.), *Models of brain function* (pp. 255–272). New York: Cambridge University Press.
- Gibson, J.J. (1979). *The ecological approach to visual perception*. Hillsdale, NJ: Erlbaum.
- Grossberg, S., & Grunewald, A. (1997). Cortical synchronization and perceptual framing. *Journal of Cognitive Neuroscience*, 9, 117–132.
- Hay, J.C., & Goldsmith, W.M. (1973). Space-time adaptation of visual position constancy. *Journal of Experimental Psychology*, 99, 1–9.
- Held, R., & Durlach, N. (1993). Telepresence, time delay and adaptation. In S.R. Ellis, M.K. Kaiser, & A.C. Grunwald (Eds.), *Pictorial communication in virtual and real environments* (pp. 232–246). London: Taylor and Francis.
- Held, R., Efstathiou, A., & Greene, M. (1966). Adaptation to displaced and delayed visual feedback from the hand. *Journal of Experimental Psychology*, 72, 887–891.
- Kitazawa, S., Kohno, T., & Uka, T. (1995). Effects of delayed visual information on the rate and amount of prism adaptation in the human. *The Journal of Neuroscience*, 15, 7644–7652.
- König, P., & Schillen, T.B. (1991). Stimulus-dependent assembly formation of oscillatory responses: I. Synchronization. *Neural Computation*, 3, 155–166.
- Sestokas, A.K., & Lehmkuhle, S. (1986). Visual response latency of X- and Y- cells in the dorsal lateral geniculate nucleus of the cat. *Vision Research*, 26, 1041–1054.
- Shapley, R.M., & Victor, J.D. (1978). The effect of contrast on the transfer properties of cat retinal ganglion cells. *Journal of Physiology (London)*, 285, 275–298.
- Sheridan, T.B., & Ferrel, W.R. (1963). Remote manipulative control with transmission delay. *Perceptual and Motor Skills*, 20, 1070–1072.
- Smith, K.U., Wargo, L., Jones, R., & Smith, W.M. (1963). Delayed and space displaced sensory feedback and learning. *Perceptual and Motor Skills*, 16, 781–796.
- Smith, W.M., McCrary, J.R., & Smith, K.U. (1962). Delayed visual feedback and behavior. *Science*, 132, 1013–1014.
- Welch, R.B. (1978). *Perceptual modification: Adapting to altered sensory environments*. New York: Academic Press.

(RECEIVED 9/18/00; REVISION ACCEPTED 2/25/01)