Current Biology, Vol. 15, 1125–1128, June 21, 2005, ©2005 Elsevier Ltd All rights reserved. DOI 10.1016/j.cub.2005.05.023

Perception of the Consequences of Self-Action Is Temporally Tuned and Event Driven

Paul M. Bays,[1],* Daniel M. Wolpert,[1]
and J. Randall Flanagan[2]
[1]Sobell Department of Motor Neuroscience
Institute of Neurology
University College London
Queen Square
London, WC1N 3BG
United Kingdom
[2]Department of Psychology and
Centre for Neuroscience Studies
Queen's University
Kingston, Ontario, K7L 3N6
Canada

Summary

It has been proposed that in order to increase the salience of sensations with an external cause, sensations that are predictable based on one's own actions are attenuated [1, 2]. This may explain why self-imposed tickle [3, 4] or constant forces [5] are perceived as less intense than the same stimuli externally imposed. Here, subjects used their right index finger to tap a force sensor mounted above their left index finger. When a motor generated a tap on the left finger synchronously with the right tap, simulating contact between the fingers, the perception of force in the left finger was attenuated compared to the same tap experienced during rest. Attenuation gradually reduced as the left tap was either delayed or advanced relative to the active right tap. However, no attenuation was seen to left taps triggered by right-finger movements that stopped above or passed wide of the sensor. We conclude that there is a window of sensory attenuation that is broadly temporally tuned and centered on the time at which the fingers would normally make contact. That is, predictive tactile sensory attenuation is linked to specific external events arising from movement rather than to the movement per se.

Results and Discussion

Subjects were required to judge the relative magnitude of two taps experienced sequentially on the left index finger. The first tap (test tap) was of fixed magnitude (2.7 N), whereas the second tap (comparison tap) was varied with a two-alternative forced-choice paradigm to determine the point at which it was perceived as equal to the test tap (see Experimental Procedures and Figure 1). In a control condition, both taps were delivered while the hands were at rest. At the point of perceptual equality, the comparison tap was not significantly different from the test tap (M = 94% of test tap, standard error [SE] = 6%, $F_{1,11} = 1.0$; $p = 0.34$). In a test condition, the test tap was triggered with minimal delay when the subjects tapped their right index finger on a force sensor fixed above their left index finger. This situation simulates direct tapping onto one's own finger through a solid object. As in the control condition, subjects compared the perceived strengths of the test tap and a comparison tap that was unrelated to the tapping movement and applied to the left index finger a short interval later. In contrast to the control condition, perceptual equality was achieved when the comparison tap was substantially smaller than the test tap (M = 71% of test tap, SE = 5%) and significantly smaller than in the control condition ($F_{1,11} = 13.7$; $p = 0.004$), implying substantial attenuation of the test tap. These results are consistent with the previous finding [5] that a self-generated force is perceived as considerably weaker than an externally generated force of the same magnitude.

In addition to the trials that simulated a self-generated tap with no delay, the test condition included trials in which the time interval between the subject's active tap on the force sensor and the test tap delivered to the subject's passive finger was varied parametrically. The relative amplitude of the comparison tap to test tap for perceptual equality for each time interval is shown as the filled circles in Figure 2A. The amount of attenuation decreased with increasing temporal asynchrony, regardless of whether the test tap came before or after the active tap. When the test tap occurred 300 ms after the active tap, the maximum delay tested, the response was not significantly different from the baseline (dotted line Figure 2A) set by the control condition ($F_{1,11} = 1.3$; $p = 0.27$). When the test tap occurred in the range 200–400 ms before the active tap, a significant difference from baseline was still observed ($F_{1,11} = 5.8$; $p = 0.034$), but the level of attenuation was substantially reduced compared to the level in the zero-delay trials ($F_{1,11} = 13.4$; $p = 0.004$). Because the timing of test taps delivered before the active tap had to be predicted, for the purposes of analysis we binned the data for these trials according to the actual time delay between taps (see Experimental Procedures).

It is possible that the greatest attenuation occurred with zero delay because this was the mean temporal asynchrony experienced during the experiment. Similarly, the width of the attenuation window we have observed might result from the specific range of asynchronies experienced during the experiment. To test these possibilities, we had a second group of subjects participate in a modified version of the experiment; this version consisted only of trials in which the test tap followed the active tap, either with no delay or with delays of 100 or 300 ms. Results from this group (empty circles in Figure 2A) did not differ significantly from those in the first group ($F_{1,20} < 0.58$; $p > 0.45$), and the greatest attenuation was again seen when there was no delay, despite the change in the mean delay from 0 to 133 ms and the change in the range of asynchronies from 600 to 300 ms. We can therefore conclude that the window of attenuation is independent of the delays

*Correspondence: p.bays@ion.ucl.ac.uk

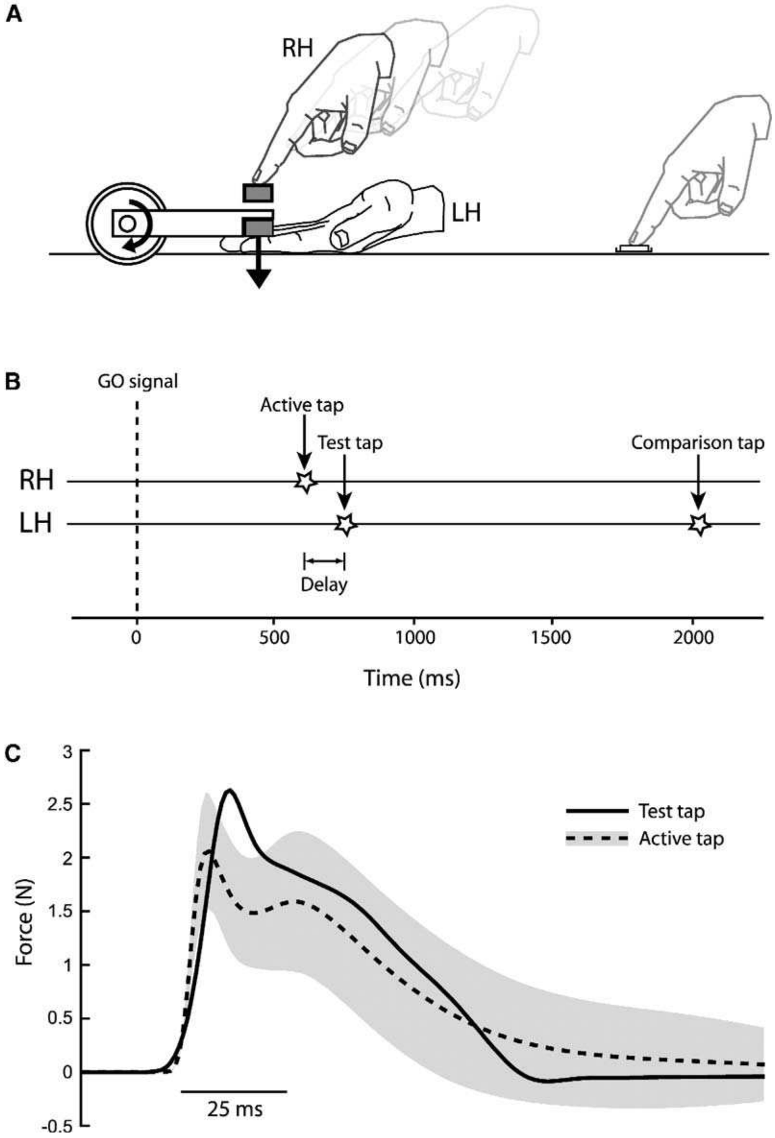

Figure 1. Apparatus and Procedures

(A) Schematic of the apparatus and task. To begin each trial, subjects depressed a button with their right index finger while resting their left index finger beneath a force sensor fixed to the lever of a torque motor. On movement trials, in response to an auditory go signal, subjects released the button and made a speeded movement to produce a brief force pulse (active tap) with their right index finger on a second force sensor fixed above their left index finger. A similar force pulse (test tap) was delivered with a variable delay to the left index finger by the torque motor.

(B) Time course of events experienced by the right and left hands (RH and LH) in an example movement trial with a +150 ms delay. The test tap was followed after a short interval by a comparison tap of variable amplitude, and subjects then indicated which of the two taps they perceived as harder.

(C) Mean force profiles of the test tap (solid line) and active tap (dashed line, gray area represents ± 1 standard deviation [SD]) on zero-delay trials. The force profiles have been aligned to force onset for ease of comparison; processing time introduced an 11 ms delay to the test tap not shown here (see Experimental Procedures).

experienced and is maximal at the time at which the active hand contacts the surface above the passive hand.

Movement-related sensory attenuation [6] has been extensively documented by Chapman and colleagues [7]. For example, the threshold for detection of an electrical stimulus is raised in a moving finger compared to the finger at rest. However, little change in detection threshold is seen in the finger contralateral to the movement [8]. To confirm that the attenuation observed in the current study did not result from the movement alone or simply from the synchronous tactile inputs received in the two fingers, a third group of subjects was tested. For these subjects, the test tap was triggered either by contact with the force sensor as before or by similar right-finger movements that stopped just above or passed in front of the force sensor. Significant attenuation was observed only when the movement resulted in contact (comparison to no-movement condition: $F_{1,7} = 6.8$; $p = 0.035$; Figure 2B). In addition, no significant attenuation was seen when synchronous taps were experienced by both fingers in the absence of movement. These results suggest that the attenuation seen when one finger strikes another is the result of a predictive mechanism rather than being related to either movement or synchronous sensory inputs alone.

Consistent with a previous study of tactile sensory attenuation [5], we have demonstrated substantial attenuation in the perceived intensity of a self-generated tap made by one finger on a finger of the other hand. This attenuation may result from a mechanism that predicts the sensory consequences of self-generated actions on the basis of planned motor activity and attenuates it from the incoming sensory stream [5, 9, 10]. We have also mapped out the time course of this predictive tactile attenuation and found a roughly symmetrical and relatively broad period of attenuation centered on the precise time at which the action would normally cause a tactile sensation. This result is consistent with

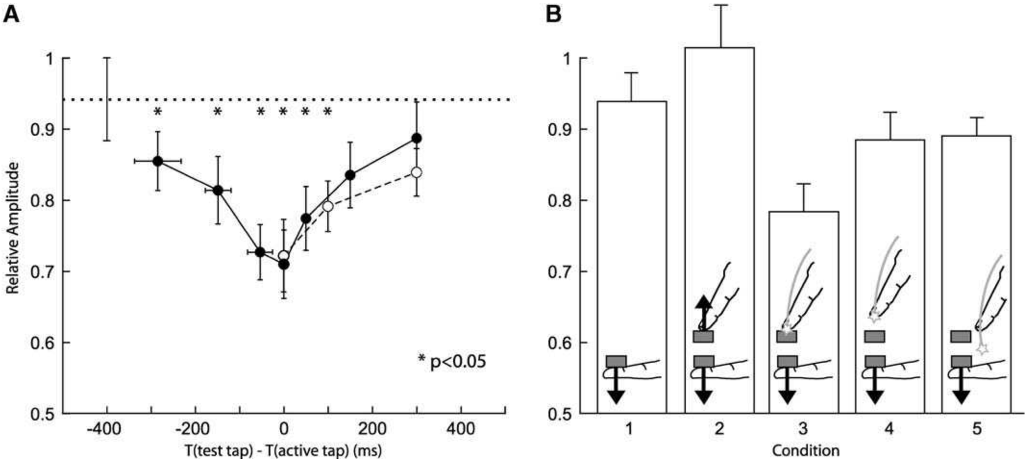

Figure 2. Mapping the Time Course of Tactile Sensory Attenuation

(A) Relative amplitude of the comparison tap to the test tap at the point of perceptual equality, as a function of asynchrony between test tap and active tap. Filled circles show mean relative amplitude for group A, empty circles for group B. The dotted line shows mean relative amplitude for group A in the no-movement condition. Vertical error bars represent ±1 SE. In the case of negative asynchronies, the position on the abscissa represents the mean asynchrony over all trials within the corresponding timing bin (see Experimental Procedures), and horizontal error bars represent ±1 SD. Asterisks indicate asynchronies at which the relative amplitude was significantly different ($p < 0.05$) from that observed in the no-movement condition of group A.

(B) Mean relative amplitude as a function of experimental condition for subjects in group C. Error bars represent ±1 SE. Insets illustrate the position of the right finger at the time at which the test tap is triggered. Gray lines illustrate the movement path of the right fingertip with stars indicating the movement endpoint. Arrows represent force pulses delivered by the torque motors. See text for full details.

a previous study [9], which found that an artificially introduced delay of 300 ms was sufficient to abolish the attenuation of a self-generated tickle and that smaller delays produced a partial reduction in attenuation. However, in this previous study, the delay was introduced between a continuous movement of the active hand and an identical movement of the stimulus on the passive hand. This meant that, even when a delay was present, there was a strong relationship between the activity of the active hand and the simultaneous sensation in the passive hand. This would tend to obscure the actual time course of attenuation. In contrast, when a time delay was introduced in the current study, there was little or no overlap between the force-generating activity in the active hand and the sensation in the passive hand. These results provide evidence for precise predictive sensory attenuation that does not result from either movement or sensation in the active effector alone but rather is linked to task-specific events predicted to arise as the consequence of an action.

Experimental Procedures

After providing written informed consent, 30 right-handed subjects (20 men and 10 women) aged 18–40 participated in this experiment as follows: 12 in group A, 10 in group B, and 8 in group C. A local ethics committee approved the experimental protocols. Each subject rested his or her left index finger in a molded support beneath a lever attached to a torque motor (Figure 1A). To start each trial, subjects depressed and held a start button with their right index finger.

For group A, there were eight different trial types, each occurring once every eight trials in a pseudorandom order. The eight types included one no-movement trial and seven movement trials. On no-movement trials, subjects continued to hold down the start button while two taps, separated by an interval of 800–1500 ms, were sequentially delivered (test tap followed by comparison tap) to their left index finger by the torque motor. Subjects then pressed one of two response buttons to indicate which of the two taps they perceived as harder. The peak force amplitude of the second comparison tap was varied across trials according to a maximum-likelihood procedure (see below) so as to find the amplitude at which it was perceived as equal to the first test tap, which always had a fixed amplitude of 2.7 N. Both taps had a fixed duration of 80 ms.

On movement trials, after an auditory go signal, subjects released the start button and made a speeded movement (amplitude 14 cm) to tap with their right index finger on a force sensor fixed above, but not in contact with, their left index finger (active tap, Figure 1A). As in the no-movement trials, two taps were delivered to the left index finger, and subjects indicated which they perceived as harder. The test tap came at one of seven different delays compared to the active tap: −300, −150, −50, 0, +50, +150, and +300 ms, with a positive delay indicating that the passive finger experienced the force pulse after the active finger contacted the surface. On the 0 ms delay trials, the test tap was triggered by the subject's active tap on the force sensor with almost zero delay (CPU processing time and the dynamics of the torque motor introduced a small delay of approximately 11 ms). On positive-delay trials, the test tap was again triggered by the active tap, but with a fixed delay of 50, 150, or 300 ms (Figure 1B). On negative-delay trials, the test tap occurred a set time after the go signal so as to occur 50, 150, or 300 ms before the predicted time (based on the median interval between the go signal and active tap on previous trials) of the active tap. The mean interval between go signal and active tap during the experimental session was 651 ms. Subjects in group A completed a total of 400 trials. Subjects in group B participated in an identical experimental protocol, but with only three trial types, consisting of delays of 0, +100, and +300 ms. Subjects in this group completed a total of 300 trials, 100 in each condition.

To ensure that the test tap was similar in size to the active tap even when it came in advance, we fixed the amplitude of the test pulse at 2.7 N and trained subjects in an earlier practice session to produce an active tap with a similar force amplitude. During the experimental session, any trial in which the amplitude of the subject's active tap fell outside the range of 1.75–3.50 N was rejected and the trial was repeated. During the experimental session, the active tap had mean amplitude 2.40 ± 0.35 N (Figure 1C; forces sampled online at 1000 Hz).

Subjects in group C completed five consecutive experimental conditions in a pseudorandom order (illustrated in Figure 2B). The position of the tip of each subject's right index finger was recorded online with an Optotrak 3020 motion-analysis system (Northern Digital, Waterloo, Ontario) at 150 Hz. Condition 1 consisted of 50 no-movement trials identical to those described above for group A. Condition 2 was identical to condition 1 except that the subject's right index finger was held above and in contact with the upper force sensor in a molded support, and an upward force pulse (2.4 N, 80 ms) was delivered to the right index finger synchronously with the test tap on the left. Condition 3 consisted of 50 trials identical to the 0 ms delay trials in group A, i.e., the test tap was triggered by the right index finger tapping on the force sensor. Condition 4 was identical to condition 3 except that subjects responded to the go signal by making a right-finger movement that stopped just above the force sensor; the test tap was triggered when the downward speed of the finger fell to zero. In condition 5, at the go signal, subjects made a tapping movement 4 cm in front of the force sensor but did not make contact; the test tap was triggered when the fingertip passed through the horizontal plane coincident with the top surface of the force sensor.

We used a maximum-likelihood procedure to determine the peak force amplitude of the second comparison tap for a given trial. At the end of each trial, the comparison-tap amplitude and the subject's response on that trial were pooled with the data from all previous trials of the same type. For group A, the negative-delay trials were each pooled into one of three bins according to the actual interval between test tap and active tap: 0–100, 100–200, and 200–400 ms. Negative-delay trials with intervals outside of the range 0 to 400 ms were rejected from further analysis. The data from each trial type were fitted with a logistic function according to a maximum-likelihood procedure, and the response threshold was calculated to estimate the comparison-tap amplitude that would make the test and comparison taps perceptually equal. A force amplitude was chosen from a uniform random distribution bounded by the 1% and 99% points on the fitted psychometric logistic curve, and this amplitude was used for the comparison tap on the next trial of the same type. In subsequent analysis, the response threshold was calculated over all responses for each subject and trial type (or bin in the case of negative-delay trials). Within-subject and between-subject comparisons among trial types were made with paired and unpaired t tests, respectively.

Acknowledgments

This work was funded by the Wellcome Trust, the Human Frontier Science Program, the Riken Brain Science Institute, and the Natural Sciences and Engineering Research Council of Canada. We thank James Ingram, Ian Howard, and Richard Symonds for technical support.

Received: January 18, 2005
Revised: April 14, 2005
Accepted: May 9, 2005
Published: June 21, 2005

References

1. Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. J. Comp. Physiol. Psychol. *32*, 482–489.
2. Von Holst, E. (1954). Relations between the central nervous system and the peripheral organs. Brit. J. Anim. Behav. *2*, 89–94.
3. Weiskrantz, L., Elliott, J., and Darlington, C. (1971). Preliminary observations on tickling oneself. Nature *230*, 598–599.
4. Claxton, G. (1975). Why can't we tickle ourselves? Percept. Mot. Skills *41*, 335–338.
5. Shergill, S.S., Bays, P.M., Frith, C.D., and Wolpert, D.M. (2003). Two eyes for an eye: The neuroscience of force escalation. Science *301*, 187.
6. Angel, R.W., and Malenka, R.C. (1982). Velocity-dependent suppression of cutaneous sensitivity during movement. Exp. Neurol. *77*, 266–274.
7. Chapman, C.E., Bushnell, M.C., Miron, D., Duncan, G.H., and Lund, J.P. (1987). Sensory perception during movement in man. Exp. Brain Res. *68*, 516–524.
8. Williams, S.R., Shenasa, J., and Chapman, C.E. (1998). Time course and magnitude of movement-related gating of tactile detection in humans. I. Importance of stimulus location. J. Neurophysiol. *79*, 947–963.
9. Blakemore, S.J., Frith, C.D., and Wolpert, D.M. (1999). Spatiotemporal prediction modulates the perception of self-produced stimuli. J. Cogn. Neurosci. *11*, 551–559.
10. Wolpert, D.M., and Flanagan, J.R. (2001). Motor prediction. Curr. Biol. *11*, R729–R732.