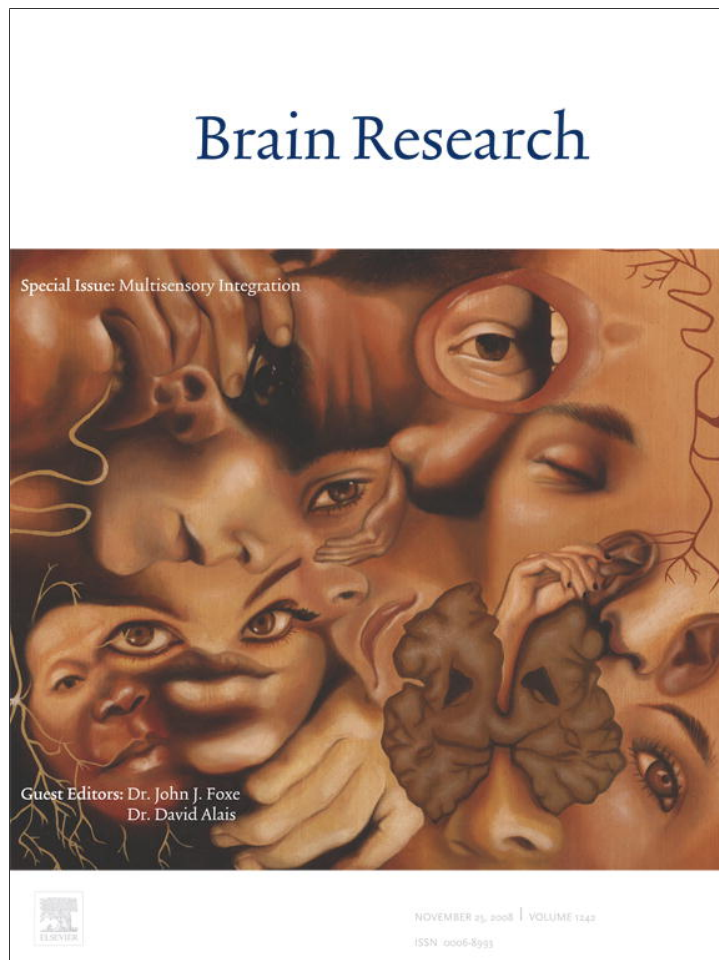


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available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****The relative timing of active and passive touch***Rebecca Winter**, Vanessa Harrar, Marta Gozdzik, Laurence R. Harris

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ABSTRACT

Tactile stimulation usually occurs as a combination of an active movement (reaching out to touch a surface) and a sensation (actually feeling the surface against the skin). The brain has information about the active component (the motor command) before it occurs because of efference copy, while the passive component must be transduced before it can be processed. Since the active and passive tactile components are available to the brain at different times, determining the time of touch requires calculation worked backwards from the passive sensation, and/or worked forward from the active motor command. In order to determine which touch process is perceived more quickly, we varied the relative delay between an active and a passive touch signal and determined the relative time perceived as simultaneous. A passive touch needed to be presented before an active key was pressed in order for the two touches to be perceived as simultaneous, but this timing difference was not significant. In order to test the plasticity of the active and passive touch systems, we exploited the fact that the point of subjective simultaneity between two stimuli can sometimes be altered by repeated exposure to asynchronous presentation. We exposed subjects to an active key press/ passive touch pair delayed by 250 ms. This exposure increased the range of relative delays between active and passive touches at which the pairs were judged as simultaneous. This is consistent with an adaptive change in the processing of active touch.

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1. Introduction

When a person reaches out and touches something there are two aspects to the event: the plan to reach out, and the sensory feedback once the action is completed. The plan consists of a decision to make the movement and an intention to move a part of the body from one place to another. This plan is then converted into a series of muscle activations which eventually carry out the movement. A copy of the motor command is available to many parts of the brain even before the movement occurs. This copy is known as the efference copy (von Holst and Mittelstaedt, 1950). In contrast, sensory feedback can only occur following the movement.

Libet et al. (1983) suggest that the efference copy for an active movement occurs as long as 250 ms before the movement. Efference copy can therefore be used to predict the timing of an action and to make anticipatory compensations (Duhamel et al., 1992; Morrone et al., 2005). In touch, an “active movement”, with its accompanying efference copy, may have an advantage in being able to predict the time of contact, over “passive touch” which only has sensory feedback (Kornhuber and Deecke, 1965). The anticipation of the active movement might allow for compensation in the neural delays which are inherent in the tactile system when determining the timing of a touch sensation.

When trying to determine when sensory stimuli were experienced (such as when making temporal order

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judgments), the relative timing of the stimuli needs to be reconstructed in memory (Libet et al., 1983; Lau et al., 2004). Obviously this reconstruction occurs after the event, but perhaps it could be done more accurately with the aid of efference copy. Therefore we want to determine the relative timing of the perception of the time of occurrence of an active key press (with efference copy) and a passive touch (with only the feedback from the touch). Would the active key press be perceived to be felt before the passive touch as a result of its efference copy advantage? Or would the sensory component of an active key press be unaffected by the fact that it is the consequence of a motor act? Currently, there are no published studies that have tested the perceived timing between active and passive touches. We hypothesize that, in order for an active and passive touch to be perceived as simultaneous, the passive touch will need to occur before the active key press to make up for the hypothesized backwards displacement in time enabled by the efference copy.

Since the efference copy is available up to 250 ms before the event and the sensory feedback arrives in the brain some 40 ms after the event (Macefield et al., 1989), matching the timing of the two requires a flexible system. Previous experiments have found that after repeated exposure to asynchronously presented multisensory stimulus pairs, the timing at which the stimuli are perceived as simultaneous can change (Fujisaki et al., 2004; Vroomen et al., 2004; Harrar and Harris, 2005). Changes can be found in both the PSSs (point of subjective simultaneity) and JNDs (just noticeable differences: the range of relative times perceived as simultaneous). A JND increase corresponds to a widening of the temporal window of stimulus staggers that are accepted as simultaneous. A PSS shift corresponds to a new estimate of simultaneity.

As the efference copy provides these active movements with additional information, it might be expected that active movements would be less responsive than other multisensory systems to sensory feedback, indicating a need for recalibration. Stetson et al. (2006) paired an active touch with a light presented with a delay of 135 ms and found a PSS shift towards light first, treating this new delay as the new simultaneity. Similarly, Cunningham et al. (2001) found the temporal perception of an active touch system to be adaptable in response to realistic and complex delayed stimuli. These observations suggest that the active system may indeed be as flexible as the processing of multisensory stimuli.

The perceived timing of passive touches however does seem to be determined more rigidly (Harrar and Harris, 2008). Navarra et al. (2007) found only a small JND increase after repeated exposure to audio-tactile pairs with an auditory stimulus leading by 75 ms. Although Keetels and Vroomen (2008) found a small PSS shift in the direction of the exposed temporal stagger following exposure to staggered visuo-tactile pairs, it is unknown if pairing a time-staggered active and passive touch will result in a recalibration. Previous experiments have shown that recalibration can result in the misordering of two passive stimuli. Therefore, here, a recalibration could result in the perception that subjects hit the key before they actually did.

Can the temporal perception of an active touch be recalibrated in a similar way to what has been demonstrated for the

temporal perception of passive multisensory stimuli? Is the temporal perception of the efference copy as flexible as the temporal perception of sensory feedback?

Given that previous experiments show some flexibility in both the active and passive touch systems, we hypothesize that following exposure there will be some change in either JND or PSS of an active and passive touch pair.

2. Results

The PSS, at which active and passive touches were most likely to be perceived as occurring at the same time, was -29.0 ms (SE 14.5; where negative means the passive touch needed to occur first). This value was not significantly different from true simultaneity ($t_{11} = -1.702$, $p = 0.117$). The JND, defined as the standard deviation of the fitted Gaussian (see Experimental procedures), was 104.7 ms (SE 13.4). These data are shown in Fig. 1 for each subject and for the mean.

After exposure to 2 min of an adaptation regime in which active key presses were followed by a time-staggered passive touch 250 ms later, the PSS was not significantly altered (pre-exposure PSS = -29.0 (SE 14.7); post-exposure PSS = -28.7 (SE 14.0); $t_{11} = -.022$, $p = 0.93$). A paired samples t -test was also conducted on the standard deviations of the Gaussians (i.e., the JNDs). The JND was significantly increased after the exposure (pre-exposure JND = 104.7 ms (SE 13.4); post-exposure JND = 129.6 ms (SE 13.2); $t_{11} = -2.735$, $p = 0.019$). These comparisons are illustrated in Fig. 2.

3. Discussion

The active key press seemed to be perceived slightly before a passive touch, but this difference was not significant. The 29 ms advantage found here is exactly consistent with the

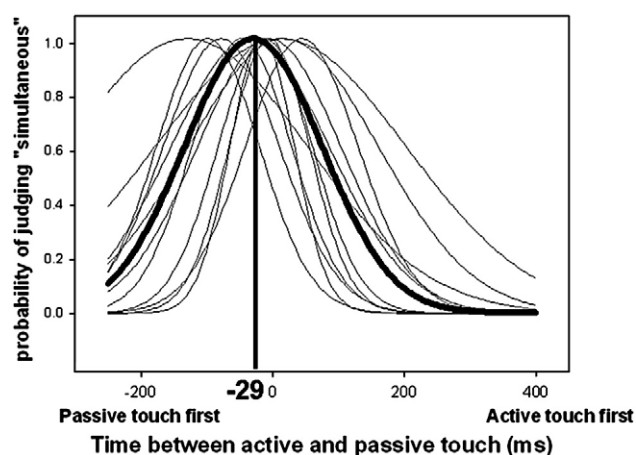


Fig. 1 – The probability of judging an active key press and passive touch as simultaneous plotted as a function of the time delay between them. The best fit Gaussians for each subjects' probability distribution are shown by the thin lines. The best fit to the average is shown by the fat line. The delay time that was most likely to be chosen as synchronous is indicated by the vertical line.

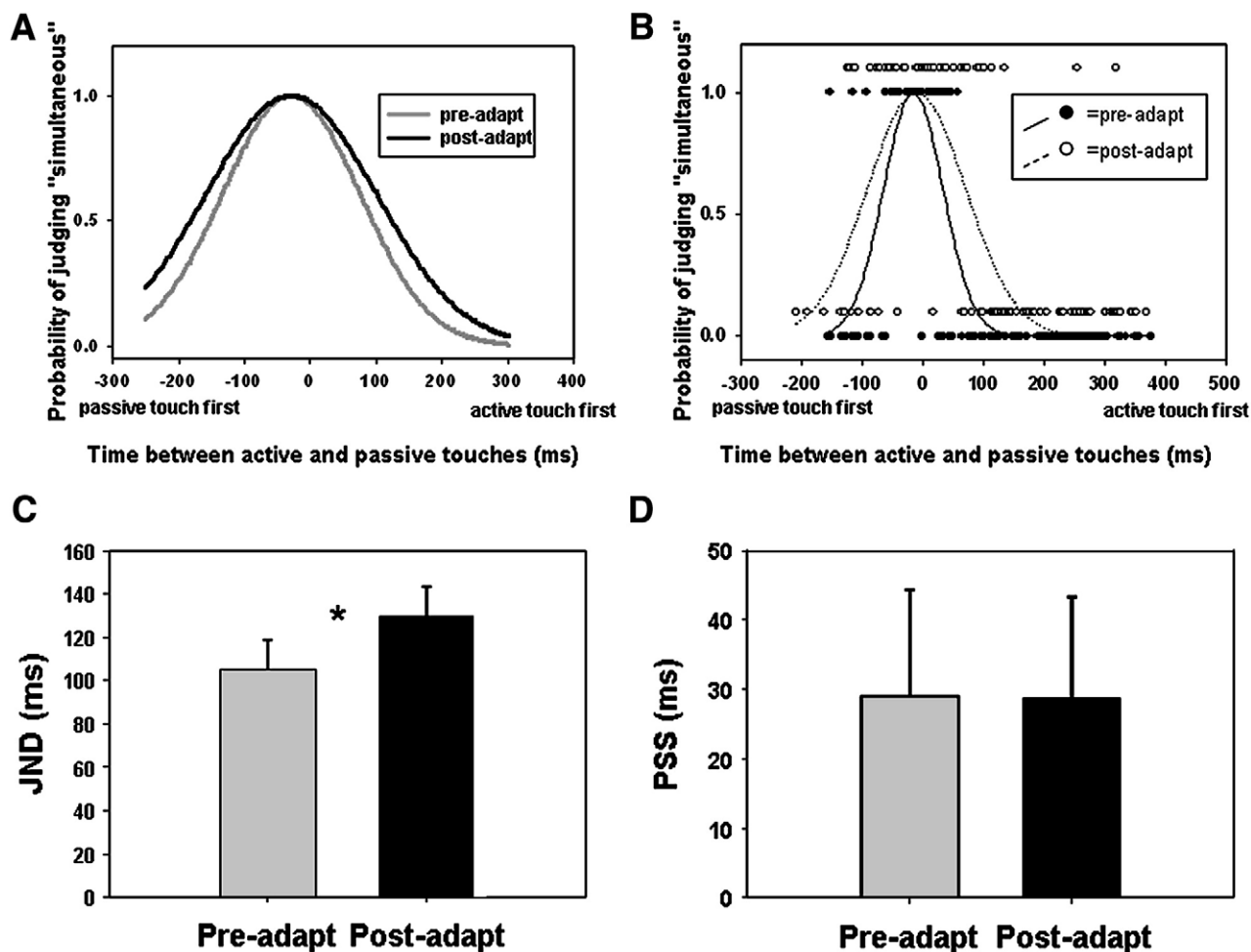


Fig. 2 – Adaptation to temporally staggered active–passive touches. (A) shows the “pre-adapt” (black line) and “post-adapt” (grey line) probability of judging active and passive touches as simultaneous as a function of the time between them generated by averaging all twelve subjects’ data. (B) shows the data from one typical subject. The circles show responses: “simultaneous” has a value of 1.0 and “not simultaneous” had a value of 0. Filled circles indicate judgments made pre-adaptation, open circles indicate judgments made post-adaptation. (Note that the open circles have been displaced vertically for clarity). The best fit Gaussians for this subject’s data are plotted through these two data sets (solid line — pre-adapt, dashed line — post-adapt). (C and D) are histograms comparing the JNDs and PSSs, respectively, from pre-(grey) and post-(black) adapt probability distributions. * indicates significant at the $p < 0.05$ level. Standard errors of the means are also shown.

29 ms advantage that Lau et al. (2004) found when judging the onset of movements relative to a clock used as an external visual reference. However, the 29 ms difference is not significantly different from 0 (in neither the present experiment nor in Lau et al. (2004)).

Previous studies have shown that sensation during an active movement is suppressed (Williams et al., 1998). If suppression were total this would mean that when the active and passive touch stimuli were presented simultaneously subjects would only be experiencing the passive stimulus while suppressing the sensation felt when hitting the active key. A study conducted by Haggard and Whitford (2004) suggests that complete suppression of sensation is either unlikely or that the sensation is actually enhanced. The study found that subjects perceived a weaker sensation following voluntary action versus an involuntary action, but the voluntary sensation was not completely eliminated. Haggard

and Whitford (2004) also suggest that while sensation of the voluntary action is suppressed, the sensation of the goal (i.e., hitting a key) is actually enhanced.

It should be noted that different types of stimuli were used for active and passive touch in this experiment. To control for this, future studies can be done with the same key for the active and passive conditions; in the passive condition the key would move up to hit a subject’s hand. In this way, the cutaneous stimulation can be arranged to be exactly the same for the active and passive conditions.

After exposure to a time-staggered active–passive touch pair, we found that the PSS did not change, but the JND became significantly larger. These observations are consistent with the study of Navarra et al. (2007) which showed that, following adaptation to asynchronous audio-tactile pairs, there was no PSS change but there was a significant increase in the JND. Navarra et al. (2007) suggested that a JND increase

might be the first stage of a temporal recalibration, which may later be followed by a shift in PSS, if the adaptation regime is maintained (Harris et al., *in press*). Other passive multisensory stimulus combinations have been shown to adapt, revealing large shifts in the PSS following exposure to time-staggered pairs. In particular, the audio-visual system seems especially flexible (Vroomen et al., 2004; Fujisaki et al., 2004; Harrar and Harris, 2008) perhaps related to the fact that the audio-visual simultaneity constancy system (Kopinska and Harris, 2004) has to regularly adjust for the large delays that often occur naturally between the audio and visual correlates of a single event. On the other hand, the temporal relationship between active and passive touches is more fixed and reliable for a given body part. This could lead to the touch system being more rigid and less likely to recalibrate (i.e., less likely to show a PSS shift) in response to external demands. In a rigid system only the first stage of recalibration (i.e., a JND increase) would be likely after a short exposure to time-staggered stimuli.

The results of this study suggest that efference copy does not give the perceived timing of an active touch a significant advantage over the perceived timing of a passive touch. The temporal perception of touches seems to be more rigid than for other sensory systems; however, changes in the perceived relative timing of active and passive touches can be induced.

4. Experimental procedures

4.1. Subjects

Subjects for both experiments were volunteers from York's undergraduate and graduate faculties. Some subjects were paid for participating. All subjects gave informed consent and all experiments were approved by York University's ethics board. There were 13 subjects (8 males, 5 females mean age 23), and all but two subjects were right handed. One subject was removed as a result of high DFFITS (difference between fitted values > 1) when an outlier analysis was conducted.

4.2. Passive touch

The passive touch stimulator was made from a small solenoid with an attached probe mounted in a 4 × 2 × 2 cm wooden cup which hid the touch from view. When the solenoid was powered, the probe was pushed out. The probe extended about 1 mm from the edge of the cup and hit the skin surface with the force of a gentle tap spread over a surface area of about 1 mm². The solenoid was controlled by appropriately amplified, 5-volt signals from a CED1401 interface box controlled by a PC. The solenoid took 5 ms to extend and to retract back into its wooden cup as measured by a carefully positioned photocell (experiments were arranged so that the delay did not affect any of the results.) The wooden cup with a touch stimulator inside was taped onto the glabrous skin at the tip of each subject's left index finger. The position of the solenoid was adjusted until subjects felt the tap from it. Stimulus duration was always 40 ms. Subjects also wore headphones which generated white noise (David Clark co., model 10a) to block out the slight click generated by the solenoids when activated.

4.3. Active touch

The active touch stimulator was a Morse code key which gave an 'on' signal when the key was pressed and the circuit was connected. Subjects were instructed to keep their right finger about 5 mm above the key between trials.

4.4. Procedure

Subjects sat in a well-lit room with their left hand (with the passive touch) resting on the desk palm up and their right hand hovering above the key. Each hand was about 12 cm on each side of an LED 50 cm from the subject. Subjects were instructed to hit the touch key as soon as the LED ("go light") flashed on for 40 ms. Trials in which the subject took longer than 400 ms to hit the key were discarded.

The passive touch stimulus, on their left index finger, was presented between 10 and 450 ms after the "Go light" (see Fig. 3A). This range was selected to ensure that active key press would sometimes be before and sometimes after the passive touch on different trials. The time it took the subject to press the key was recorded as the reaction time (RT). The average reaction time of the key press across subjects was about 230 ms. After the experimental session, the relative time between the active key press and the passive touch was calculated by subtracting the RT from the onset of the passive touch for each condition and for each subject. Thus positive relative values correspond to the active key press occurring

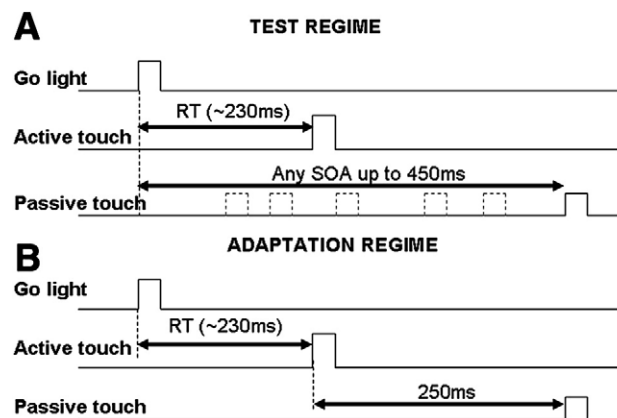


Fig. 3 – (A) Test regime. Subjects pressed the key (active touch, second row) in response to the onset of the "Go light" (top row). The time it took the subject to press the key was recorded as the reaction time (RT). The passive touch (third row) occurred between 10 and 450 ms after the "Go light" and therefore occurred at a range of times relative to the active touch (from about 220 ms before to about 220 ms after the active key press). The relative time between the active key press and the passive touch was calculated offline by subtracting the RT from the onset of the passive touch for each trial. Thus positive values correspond to the active key press occurring first, and negative for passive touch occurring first. **(B) Adaptation regime.** Subjects pressed the key at the onset of the "Go light". A passive touch was triggered from the key press and presented 250 ms later (layout as for A).

before the passive touch and negative for passive touch occurring before the active. There were 120 trials.

After each active key press and passive touch combination, subjects reported whether the two touches appeared either “simultaneous” or “not simultaneous”. By lifting their left foot they reported “simultaneous” and by lifting their right foot they reported “not simultaneous”.

4.5. Recalibration procedure

In the recalibration condition subjects pressed the active key, after the “go light” and received the passive touch 250 ms after pressing the active touch key as shown in Fig. 3B. This stimulus combination was repeated for 2 min with a variable inter-pair delay of 750 ms–1.5 s. In this two-minute period there were typically 120 time-staggered pairs presented. Subjects were then presented with random-delay times in which the passive touch could come on first or second (see above) and reported their perception of simultaneity. After every random-delay trial subjects would be presented with a “top-up” trial (another presentation of the exposure delay of 250 ms). Subjects had to respond either simultaneous or not simultaneous during the experimental and top-up trials, although responses were only recorded for experimental trials.

4.6. Data analysis

Judgments of simultaneity were assigned the value one, and not simultaneous judgments the value zero. These responses (1 or 0) were plotted as a function of the delay between the active key press and the passive touch (see Fig. 2B). A Gaussian was fitted to the data for each subject for each condition (before or after exposure) using the formula:

$$f = 1 * \exp(-0.5 * ((x - x_0) / b)^2)$$

where x_0 is the peak of the Gaussian (i.e., PSS), and b is standard deviation. We define the JND to be equal to the standard deviation of the Gaussian (i.e., the range of delays where the stimuli were regarded as simultaneous 84% of the time).

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