

Enhanced Tactile Performance at the Destination of an Upcoming Saccade

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Summary

Previous work has demonstrated that upcoming saccades influence visual [1, 2] and auditory [3] performance even for stimuli presented before the saccade is executed. These studies suggest a close relationship between saccade generation and visual/auditory attention. Furthermore, they provide support for Rizzolatti et al.'s [4, 5] premotor model of attention, which suggests that the same circuits involved in motor programming are also responsible for shifts in covert orienting (shifting attention without moving the eyes or changing posture). In a series of experiments, we demonstrate that saccade programming also affects tactile perception. Participants made speeded saccades to the left and right side as well as tactile discriminations of up versus down. The first experiment demonstrates that participants were reliably faster at responding to tactile stimuli near the location of upcoming saccades. In our second experiment, we had the subjects cross their hands and demonstrated that the effect occurs in visual space (rather than the early representations of touch). In our third experiment, the tactile events usually occurred on the opposite side of upcoming eye movement. We found that the benefit at the saccade target location vanished, suggesting that this shift is not obligatory but that it may be vetoed on the basis of expectation.

Results and Discussion

Eye movements have a strong effect on visual perception because they shift the sensitive and cortically over-represented fovea to different regions of space. Interestingly, there is clear evidence that upcoming saccades influence visual performance – with visual stimuli at the location of the saccade destination being processed more rapidly and accurately than at other locations with a similar retinal eccentricity [1, 2, 6–8]. These behavioral findings in humans complement single-cell recording in the parietal cortex and superior colliculus of primates, where neuronal firing in response to a visual stimulus is enhanced immediately prior to a saccade to the stimulus' location [9–11]. It is clear that, in addition to their role in visual perception, eye movements can influence other modalities. For example, Rorden and Driver [3]

report that performance on auditory tasks also improves at the destination of an upcoming saccade. That study complements a single-cell-recording finding by Hikosaka and Wurtz [12], who reported presaccadic enhancement to auditory stimuli. In particular, they noted that some neurons in the substantia nigra pars reticulata significantly reduce their firing rate after exposure to contralateral auditory stimuli. This reduced firing rate is sustained after the offset of brief auditory stimuli only in trials in which a saccade is made to the location of the auditory stimuli. This work demonstrates that upcoming eye movements can modulate neural firing to nonvisual stimuli. However, it is also important to note that regions of both the parietal cortex and the superior colliculus are sensitive to visual, auditory, and tactile stimuli [13], although investigators have yet to specifically look for auditory or tactile saccadic enhancement in these regions.

To date, there are no reports that tactile performance is improved by upcoming saccades. In a thorough review of the literature on crossmodal spatial attention, Driver and Spence [14] presented a schematic diagram showing all the investigated links in exogenous covert attention; however, their diagram of recent research contains a single question mark, regarding the relationship between saccade generation and touch. This question is of special importance for a number of reasons. First of all, Rizzolatti and colleagues' influential premotor model of attention [4, 5] predicts that eye movement programming will generally influence perception in all modalities. They suggest that motor circuits govern the attentional system. According to this model, in order to covertly attend to a region (pay attention to an area we are not fixating), the brain simply programs an eye or arm movement to that location. One strong prediction of this model is that preparing an eye movement will shift attention prior to the onset of the saccade. Therefore, looking for presaccadic shifts in tactile performance is an effective test of the premotor model. In addition, examining how eye movements influence tactile perception is of particular importance because it allows us to investigate how touch is remapped with changes in posture. For example, if an eye movement is programmed toward the left, is touch facilitated on the left hand or on the left side of space? One way to test this is to have the participants cross their hands, so a left eye movement will be toward the right hand.

We investigated the effects of upcoming saccades on tactile judgements. The participants made left or right eye movements in response to a symbolic central cue. They were also asked to make a speeded verbal response regarding whether they felt a tap to the proximal or distal location of either hand (responding “down” or “up,” respectively). Note that the response to the tap was orthogonal to the direction of the eye movement. Depending on the speed of the eye movement, the tap came before, during, or slightly after the saccade. Of critical importance to this study are trials where the tap occurred immediately before an eye movement—when

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Figure 1. Experimental Setup

The participants wore an eye monitor mounted to a headband. During each trial they made an eye movement from a central fixation point either to the left or to the right. The saccade destinations were illuminated by small yellow peripheral LEDs that remained on continuously (these are shown as open circles on each hand). A set of central LEDs (shown enlarged for detail) indicated the direction of the requested saccade. In addition, during each trial the subject was asked to report whether they were tapped on one of their index fingers (“up”) or on their hand (“down”). Filled circles indicate the locations of the four tappers.

saccade programming had begun but before the eye had moved. The premotor model of attention suggests that performance will be better for stimuli appearing near the destination of a saccade, regardless of the

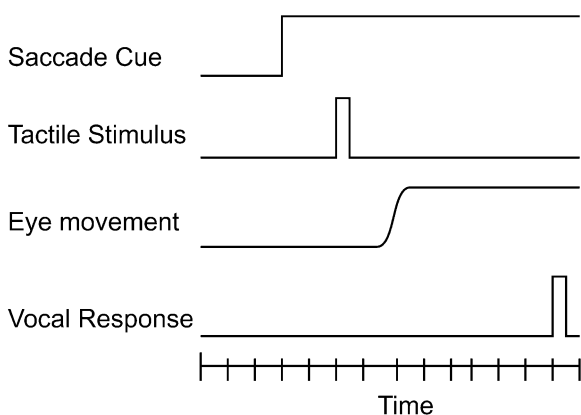


Figure 2. Timeline Showing a Typical Sequence of Events, with the Increments along the Horizontal Axis Representing 100 ms Units. Each trial was initiated by the central saccade cue being illuminated. This symbol instructed the participant to shift his/her gaze to the left or right side. After either 200 or 500 ms, a tap was delivered to one of the hands. During the critical trials, an eye movement was initiated within 200 ms of the offset of the tactile stimulus. After the saccade, the subject made a vocal discrimination regarding whether the tap was delivered to a proximal or distal location on the hand (typically within 800-900 ms of the onset of the tactile stimulus).

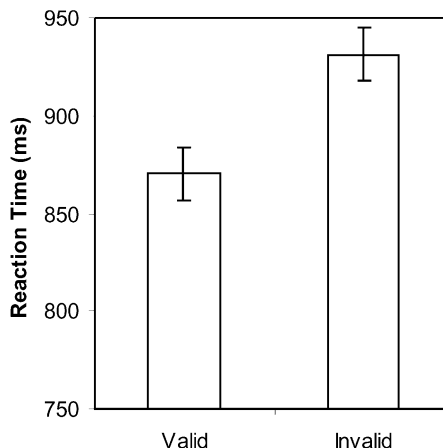


Figure 3. Mean Reaction Time Averaged across Target Location as a Function of Whether the Target was Presented at the Location of an Upcoming Saccade or at the Opposite Side of the Saccade

Trials in which the target and upcoming saccade location were the same are considered “valid,” and trials in which the target was presented at the opposite side of the saccade are considered “invalid.” The error bars show 95% within-subject confidence intervals, as suggested by Loftus and Masson [29].

modality (visual, auditory, or tactile) of the stimuli. The basic layout is illustrated in Figure 1, with a typical timeline for events shown in Figure 2. We found that responses were significantly faster if a tap occurred at the destination of an imminent saccade (valid trial) rather than at the opposite side (invalid trial). The mean vocal reaction time (RT) for valid trials was 870 ms, compared to 931 ms for invalid trials. This difference proved statistically significant with a paired t test, $t(19) = 4.39$, $p < 0.001$. This effect is shown in Figure 3. However, no difference was observed for the error rate (4.5% of valid trials, and 3.6% of invalid trials, $t(19) = 0.75$, $p < 0.464$), so the effect cannot be explained by a simple speed-error tradeoff. Because we were examining only vocal responses that occurred after an eye movement, we needed to check that the eye-movement latencies were equivalent between valid and invalid trials so as to demonstrate that the effect found on vocal responses could not be attributed to differences in eye movement latency (e.g., if eye movements are slower in the invalid condition, this delay may be transmitted to the subsequent vocal responses; this would reflect a delay in saccade generation rather than in vocal responses per se). Analysis of the eye movement latencies did not reveal a difference between the valid and invalid trials, which occurred a mean of 92.4 and 97.3 ms after the target offset, $t(19) = 1.24$, $p < 0.232$ (note that we only sampled trials where the saccade occurred within 200 ms of target offset, so there is little variability in this measure).

This experiment demonstrated that an upcoming saccade influences tactile responses. However, it is unclear whether the effect was due to a broad contralateral activation of the early somatosensory mapping [15] (e.g., a right eye movement activating not only the contralateral circuits involved with saccade generation but also the left hemisphere in general and therefore improving

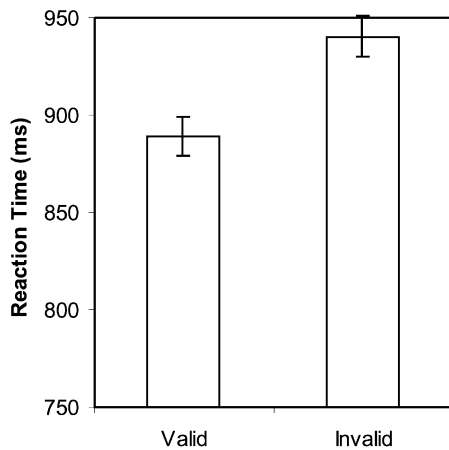


Figure 4. Mean RT and Confidence Intervals for the Crossed-Hands Condition

Here valid trials refer to trials in which tactile stimuli appeared on the same side of visual space as an upcoming saccade, e.g., left targets for a left saccade (in this example the tactile stimuli is presented to the right hand in left space).

the perception of a touch to the right half of the body) or to activation at the region of space surrounding the upcoming saccade (e.g., a right saccade improving performance to any limb near the saccade destination, regardless of whether it is a left or right arm). One way to disentangle these possibilities is to have the participants cross their hands, so the right hand is in left space and vice versa; if a right eye movement simply activates the contralateral hemisphere, one would expect it to facilitate perception on the left hand, regardless of the position of the hand. On the other hand, a number of recent studies [16, 17] have shown that shifts in tactile attention operate in the visual frame of reference. Despite these previous studies, it is possible that the effect seen in tactile perception prior to an eye movement occurs at an earlier representation than the effects seen in previous studies; therefore, we decided to test participants in an experiment identical to our first study except that they crossed their hands. Once again, we found that subjects were much faster to discriminate targets at the location of an upcoming saccade (889 ms versus 940 ms, $t(22) = 4.84$, $p < 0.001$, see Figure 4). Again, no effect was seen in error rates (2.4% versus 2.5%, $t(22) = 0.16$, $p < 0.877$) or in saccade latency across conditions (96.9 ms versus 94.1 ms after stimulus offset, $t(22) = 0.94$, $p < 0.359$). These findings clearly demonstrate that the eye movements facilitate tactile events in the region of visual space near the upcoming saccade rather than influencing a specific hand regardless of its position in space. One could argue that the crossed-hands design directly opposes any visually mapped facilitation against early-motor-representation facilitation. It is theoretically possible that both effects coexist, and therefore our finding could be taken as evidence that the visually mapped facilitation is simply the dominant factor. However, it is worth noting that the effect size found in the crossed hands experiment is of the same

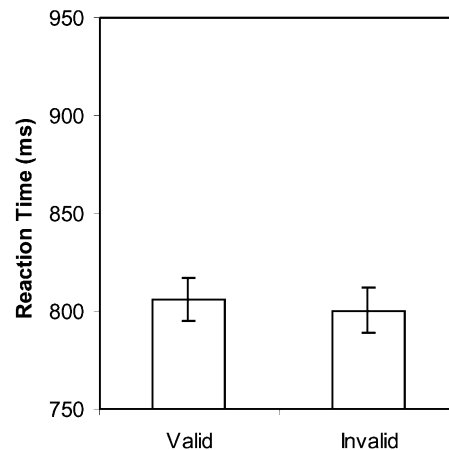


Figure 5. Mean RT and Standard Errors for the Biased Condition
As in other figures, valid trials refer to stimuli that occur at the same side as an upcoming saccade. Note that the invalid trials were three times more likely to occur than the valid trials.

magnitude as that of the original experiment. This finding suggests that the influence of early motor representation plays little role in these situations.

Finally, we were interested in whether the performance shifts observed prior to a saccade are obligatory or whether they can be vetoed by a strategic shift in orienting. It is possible that performance is always better at the saccade destination, regardless of the will of the participant. On the other hand, it is possible that eye movement control is one of a number of circuits modulating tactile performance, and so top-down control could cancel or reverse presaccadic shifts in performance. In order to examine this, we ran participants in an uncrossed-hands study in which stimuli were three times as likely to occur on the side opposite of the saccade, so that the participant had a strong incentive to try to orient tactile attention in the opposite direction of the requested saccade. In this study, subjects were not faster to discriminate targets at the location of an upcoming saccade (806 ms versus 800 ms, $t(19) = 0.51$, $p < 0.61$, see Figure 5). Again, no effect was seen in error rates (2.5% versus 3.7%, $t(19) = 1.26$, $p < 0.225$) or saccade latency across conditions (90.1 ms versus 92.6 ms after stimulus offset, $t(19) = 1.21$, $p < 0.240$). In this study, we directly pitted the effect of the upcoming saccade against any strategic control that participants could exert over their spatial attention. Therefore, we concede that we cannot rule out that the presaccadic shift did occur but that it was simply cancelled out by a strategic shift in attention. However, our result clearly shows that the effect of an upcoming saccade is not so obligatory as to supersede any other shifts in attention.

Inspection of the data across all three experiments reveals a trend for faster vocal responses in the biased-attention experiment (803 ms) compared with the crossed-hands (914 ms) and standard (901 ms) studies. In order to test this possibility, we conducted a mixed-design ANOVA with one between-subject factor (experiment type: unbiased, crossed hands, and biased) and

one within-subject factor (valid versus invalid eye movements). We found no main effect of experiment, $df(2,60) = 2.304$, $p < 0.1086$, although we found a main effect of eye-movement validity ($df(2,60) = 26.319$, $p < 0.0001$) and an interaction effect $df(2,60) = 9.063$, $p < 0.001$. The between-subjects comparison has low power because of inter-subject variance, so this null result of experiment type is difficult to interpret. One possible explanation for this potential effect might be that the strategic nature of the biased attention task leads the subjects to emphasize vocal responses in this task. Another potential explanation is that attention may be better modeled as an inhibition of unattended items rather than as a facilitation of attended items, as has been recently suggested by other authors [18]. According to this view, normal processing (in neutral conditions, without top-down control) operates at near-optimal performance, so attention operates by hindering the processing of unattended information (so the attended information has a relative competitive advantage for selection). This model could explain the trend we observed as follows: in experiments in which attentional shifts are abolished (e.g., the biased experiment, in which the participant wishes to override the reflexive presaccadic shifts), overall processing is faster than it is in conditions where attention is allowed to operate normally (e.g., the standard and crossed hands experiments). In any case, these questions do not jeopardize the primary finding of the biased attention study; it is clear that the presaccadic shifts are not obligatory.

In summary, we found that subjects were faster to discriminate tactile stimuli when the stimuli occurred near the location of an upcoming saccade. This finding supports Rizzolatti et al.'s premotor model of attention [4, 5] and highlights the tight coupling between motor programming and perception. Our crossed-hands study found that this effect remained at the location of the upcoming saccade, suggesting that a visual mapping drives this effect. Finally, our biased-attention study found that this effect vanished in blocks where the subjects expected stimuli to appear at the opposite side as the saccade. This study clearly illustrates that the presaccadic shifts in processing are not obligatory. Our findings extend previous research demonstrating that tactile stimuli attached to the index finger are detected more rapidly when participants have directed their gaze toward the stimulated hand, regardless of whether their arms are crossed or not [19].

Our own findings are nicely balanced by recent work by Doyle and Walker [20], who have shown that both auditory and tactile events can modulate the trajectory of eye movements in certain situations. They found that saccade trajectory curved away from tactile stimuli when they were task relevant (e.g., indicated the direction of a saccade, similar to an effect reported for visual stimuli [21, 22]). In addition, this pattern of curved trajectories was seen for reflexive saccades when a spatially uninformative tactile event preceded the visual target that summoned the saccade by 100 ms (their experiment 3), but not when the visual and tactile events were presented simultaneously (their experiment 2). However, it should be conceded that the spatially uninformative tactile event in their experiment 3 was always temporally

predictive of the visual target. Therefore, one conservative summary of Doyle and Walker's study is that tactile events influence saccade trajectories whenever the tactile events are relevant to the task. In any case, their work highlights the strong influence tactile events can exert on saccades and complements our present evidence for the influence of saccade generation on tactile perception.

A number of recent studies have demonstrated that noninformative vision can influence tactile sensitivity in healthy adults [23, 24] as well as in neurological patients [25]. However, each of these studies controlled for eye movements so as to remove any confound of saccades. These findings complement our own results, suggesting that eye movement programming is only one of the factors that modulate tactile perception. Our crossed-hands study suggests that tactile events are influenced by a visual frame of reference. Yamamoto and Kitazawa [26] provide another technique for assessing this mapping. They asked participants to report the temporal order of brief tactile stimuli presented in rapid succession to each hand. They found that with moderately short intervals (<300 ms) many participants reliably reported the wrong order for a majority of trials if their hands were crossed. In these conditions, the subjects were accidentally reporting the spatial location of the stimuli rather than correctly reporting which hand had been stimulated. This work suggests that tactile judgments may be initially made based on visual space, rather than based on the early-motor-representations for touch.

Recent research has demonstrated reciprocal cross-modal effects between all combinations of auditory, visual, and tactile stimuli [27]. In addition, upcoming eye movements improve perception for visual [1, 2, 6–8], auditory [3], and (as demonstrated in the present study) tactile targets occurring at the destination of the saccade. The present study suggests that the eye movements may be driving presaccadic enhancement in cross-modal circuits of the brain. We speculate that the parietal cortex and/or the superior colliculus are locations for presaccadic enhancement across modalities. This claim could be tested with single-cell recording techniques combined with the paradigm described here.

Experimental Procedures

A total of 79 participants were tested, and each was given eight short breaks during the experiment to avoid fatigue. Each individual only participated in a single experiment. Subjects were excluded from the final analysis if fewer than 12 trials were present in either the valid or invalid conditions after exclusions for errors, response outliers, blinks, and saccade latencies. A total of 29 participants were tested in the first study. Nine of these participants were rejected because of insufficient trials in the crucial conditions, yielding 20 subjects in the analysis. Twenty-eight additional individuals participated in the crossed-hands experiment, with 23 included in the analysis. Twenty-two students were tested in the biased-attention experiment, with 20 included in the analysis.

Participants were asked to move their eyes 19.5° to a peripheral light located to the left or right, as well as to judge whether a tap occurred from a proximal or distal location. They were informed that they should complete both tasks as quickly as possible. Saccade direction was indicated by a set of six red central LEDs mounted in two columns; the saccade direction cues were either the "<" (middle LED of left column, with top and bottom LED of the right

column) or the ">" symbol. Half of the participants were asked to move in the direction of the arrow (e.g., left for the "<" symbol), with the other half told to saccade toward the side with two lights (e.g., right for the "<" symbol). The saccade direction LEDs remained on for the duration of the trial and only switched off during the 300 ms intertrial interval. This counter balancing was designed to eliminate any intrinsic cuing effect of the central stimuli. Note that a seventh, yellow fixation LED located between the two columns of LEDs as well as peripheral LEDs at both possible saccade destinations were continuously illuminated. Before data collection began, all individuals trained on the eye movement task alone (approximately forty trials per individual).

Tactile stimuli were generated by four small solenoids. Two 12 volt DC solenoids were attached to the top of each hand, one on the index finger (the "up" stimuli) and the other near the base of the index finger (the "down" stimuli), as illustrated in Figure 1. The sound of the solenoids was masked by continuous white noise.

Each trial was initiated by a central set of three LEDs indicating the saccade direction. Either 200 or 500 ms after the central cue, a single 50 ms tap was delivered to one of the hands. Each trial continued until the subject either made a vocal response or 2000 ms elapsed after the offset of the tactile stimulus. After the experimenter had typed in the participant's vocal response, the participant was given 300 ms to return their gaze to the central fixation before the next trial began.

In total, there were 16 different types of conditions, with two cue-target stimulus onset asynchronies (SOAs), 200 or 500 ms, four target locations (up left, down left, up right, or down right), and two eye movement directions (left or right). The two cue-target SOAs ensured that the latency of the target was unpredictable and discouraged the participants from delaying a saccade until after the tactile stimulus. Each of these conditions was presented 15 times per block in the standard and crossed-hands experiments. For the biased-attention experiment, the invalid conditions (e.g., tap on left hand after right saccade) were presented 30 times per block, and the valid trials (e.g., tap on left hand after left saccade) were presented 10 times per block. Each subject completed 8 blocks in total for each experiment.

Eye movements were recorded with an ASL 210 eye tracker, mounted to a headband. The horizontal position of the eye was measured every 5 ms with the eye monitor's built-in 8-bit analog-to-digital converter connected to the parallel port of the computer used to display stimuli and record responses. Eye movements were identified with a simple velocity criterion (because a criterion based on position would be susceptible to signal drift); an eye movement was considered to occur when four consecutive samples exceeded 100 degrees per second. The estimated saccade latency was adjusted to account for the sampling delay caused by the eye monitor's built-in smoothing filter. Trials were rejected if the eye movement was in the wrong direction or if a blink was detected.

Participants were asked to judge the elevation of the tap by rapidly saying "up" or "down." A voice key connected to the serial port of experimental computer measured the onset of the vocal response (and recorded the latency), and the experimenter made an unsped keyboard entry of the subject's response (and recorded the accuracy). The voice key was calibrated for each individual at the start of each session and was adjusted as required to ensure accurate detection of vocal responses without false alarms. Outlier trials with reaction times outside 150–2000 ms were excluded from analysis (less than 1%). In addition, trials for which an incorrect vocal response was made were not included in the analysis of response time, although these error rates were analyzed separately to check for a modulation of performance in error rate and for speed-error tradeoffs. Only trials in which the saccade occurred within 200 ms of the offset of the tactile stimulus were included in any analysis, ensuring that a motor program was already generated for the target destination but that the valid and invalid stimuli occurred at the same retinal eccentricity. Mean rather than median reaction times were computed because some conditions included a different number of trials [28]. The mean number of trials included in the analysis per subject per condition ranged from 23.3 (valid trials in the biased experiment) to 61.3 trials (invalid trials in the biased experiment).

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