Somatosensory saccades reveal the timing of tactile spatial remapping

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Abstract

Remapping tactile events from skin to external space is an essential process for human behaviour. It allows us to refer tactile sensations to their actual externally based location, by combining anatomically based somatosensory information with proprioceptive information about the current body posture. We examined the time course of tactile remapping by recording speeded saccadic responses to somatosensory stimuli delivered to the hands. We conducted two experiments in which arm posture varied (crossed or uncrossed), so that anatomical and external frames of reference were either put in spatial conflict or were aligned. The data showed that saccade onset latencies in the crossed hands conditions were slower than in the uncrossed hands condition, suggesting that, in the crossed hands condition, remapping had to be completed before a correct saccade could be executed. Saccades to tactile stimuli when the hands were crossed were sometimes initiated to the wrong direction and then corrected in-flight, resulting in a turn-around saccade. These turn-around saccades were more likely to occur in short-latency responses, compared to onset latencies of saccades that went straight to target. The latter suggests that participants were postponing their saccade until the time the tactile event was represented according to the current body posture. We propose that the difference between saccade onset latencies of crossed and uncrossed hand postures, and between the onset of a turn-around saccade and a straight saccade in the crossed hand posture, reveal the timing of tactile spatial remapping.

Introduction

Interactions within peripersonal space, such as haptic exploration or reacting to tactile events on our skin requires the localization of touch relative to other body parts and objects in the environment. Given that body parts are movable, tactile information, which is initially represented in somatotopic (anatomical) space, must be *remapped* to refer the current position of the stimulated body part. This is essential to achieve a common reference frame that represents somatosensory information for action (for example, when smashing a mosquito against your skin), or to use during the interaction with other sensory modalities such as vision. Several results highlight the existence and relevance of this process, not only in healthy but also in brain-damaged individuals. For instance, patients suffering from tactile spatial hemineglect (or extinction) have limited conscious access to information coming from the contralesional side of the body. However, they can sometimes improve tactile detection at the affected hand just by placing it across the body midline to the ipsilesional side (Aglioti, Smania, & Peru, 1999; Moro, Zampini, & Aglioti, 2004; Smania & Aglioti, 1995). This suggests that spatial attention is at least partly expressed in an externally based reference frame, after tactile remapping has been completed.

The question addressed in this study relates to the temporal course of this remapping of touch. Some studies have indirectly hinted at relevant timings for tactile remapping. For instance, somatosensory evoked potentials in humans show that attention effects are modulated by limb posture as early as 100-140 ms after stimulation (Eimer, Cockburn, Smedley, & Driver, 2001; Eimer, Forster, Fieger & Harbich, 2004; Heed & Röder, 2010). This indicates that the remapping process must have started by that latency. Behaviourally, crossing the hands leads to systematic reversals when judging the order of two stimuli presented to each hand within less than 300 ms, as if tactile events were assigned to the anatomically (instead of externally) corresponding hand location (Wada, Yamamoto, & Kitazawa, 2004; Yamamoto & Kitazawa, 2001). In addition, Azañón and Soto-Faraco (2008a) found an inversion of spatial cueing effects of touch on vision when the hands were crossed. In particular, when the tactile cue was presented shortly before the visual target (<60 ms) responses were determined by somatotopic representations. This pattern reversed 360 ms after the tactile cue, so that facilitation occurred when cue and target were presented at coincident external locations. These findings suggest an initial representation of touch, based on a somatotopic map, followed after some hundreds of milliseconds by a referral of tactile events to an external location (see also Kitazawa, 2002). The timing of the transition between reference frames, and time it takes for the remapping process to complete, are unknown.

The goal of the current study is to investigate the time course of tactile remapping using somatosensory-directed saccades. Saccades are fast voluntary movements of the eyes made to align the fovea with objects of potential interest. Analysis of saccadic movements can provide insights into the early stages of processing, because they are elicited earlier than manual responses (Ludwig & Gilchrist, 2002). Although typically regarded as visual, saccades can also be directed to sounds or tactile stimuli. Somatosensory saccades have longer latency, lower peak velocity, and are less accurate than saccades to visual stimuli (Amlot & Walker, 2006; Blanke & Grusser, 2001; Groh & Sparks, 1996). Interestingly, Groh and Sparks (1996) reported a pilot study where the authors performed 10 saccades to somatosensory targets with the hands crossed and noticed that about 4 were initially directed to the wrong side and then quickly corrected online. These so-called turn-around saccades (TAS hereafter; van der Stigchel, Meeter, & Theeuwes, 2006) seem a straightforward, on-line, consequence of tactile remapping, reflecting the actual time at which touch is integrated with proprioception and therefore encoded in an externally based space.

We hypothesise that saccadic trajectories reflect the availability and representational format of information about target position, like it is often assumed in hand movement studies (Aivar, Brenner, & Smeets, 2008; Resulaj, Kiani, Wolpert, & Shadlen, 2009). Speeded saccadic RTs can occur as fast as 100-120 ms (e.g. Kalesnykas & Hallett, 1987), which falls within the putative time window of tactile remapping. Thus, variations in saccadic performance as a function of saccade onset variability should provide information about the timing of tactile remapping. In particular, we expect that saccade trajectories will reflect the somatotopic (anatomical) location at early times, and an external reference frame at a later stage. Indeed, we hypothesize that these two phases would be clearly dissociated during the saccade when the two reference frames are placed in conflict, for example when the hands are crossed over the body midline.

Experiment 1

Participants were asked to direct saccades to a brief somatosensory stimulus at the ring finger of one of the two hands (unpredictable), which could be either crossed over the body midline or straight (uncrossed). Participants were instructed to respond immediately after the tactile stimulus, or else after a variable delay (>600 ms). Following previous reports (Azañón & Soto-Faraco, 2008a) we hypothesise that any potential effects of the conflict between frames of reference during remapping on the execution of saccades should occur in the immediate response condition, but not in the delayed response condition, because in the latter tactile remapping should be completed prior to saccade onset.

Method

Participants

Eight participants (6 female; 7 right-handed; mean age 25.6, range 20-37) took part in this experiment. None of the participants reported any deviations from normal tactile perception, and had normal or corrected to normal vision. All of the participants gave their informed consent prior to their inclusion in the study. The study conforms with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Design and Procedure

The participants sat with their arms, either crossed or uncrossed, resting on the table, and their ring fingers 30 cm apart, at marked locations just below the outer sides of a computer screen. Solenoid tappers were taped to the dorsal side of the distal phalanx of each ring finger. The participant's head position was stabilized by a chinrest at a distance of 40 cm of the screen, and a head-mounted Eyelink II® eye tracker recorded their eye movements (250 Hz sample rate). The arms and hands were covered from the participant’s view by a black cardboard screen. A trial started by the participant fixating a dot in the centre of the screen, followed by a 9 ms tactile stimulation of one of his ring fingers by the solenoid tapper, which feels like a small tap to the fingertip. The offset of the fixation dot (immediately after the touch, or delayed by 600-1000 ms; in different blocks) prompted the participant for response.

The task for the participant was to make a saccade to the location of the stimulus as quickly and accurately as possible, after the fixation dot disappeared.

Each participant took part in four different blocks of 100 trials, with each combination of posture (arms crossed or uncrossed) and response mode (immediate or delayed). For the whole duration of the experiment white noise was played on external loudspeakers at a level sufficient to mask the sound of the tappers. This is important, because it has been shown that saccades to auditory targets can be quite accurate, and therefore could influence our results (Yao & Peck, 1997; Zambarbieri, Schmid, Magenes, & Prablanc, 1982).

Analyses

We allocated the parts of the continuous eye tracker output that belonged to saccades based on target onset using a 5% of peak velocity threshold as a criterion for the start and end of a saccade, and then we re-checked manually whether the saccades that had been extracted started at the fixation dot and ended at one of the endpoints (screen corners). Trials with missing data points within the saccade and anticipatory saccades with an onset latency shorter than 100 ms (Kalesnykas & Hallett, 1987) were discarded (<11% of the trials overall). Onset latency was calculated from tactile stimulus onset. We calculated initial saccade direction by calculating the angle between the vertical line that runs through the fixation point and the line that connects the position of the eye, at 5% of the maximal displacement on the x-axis, and the fixation point. Saccades starting in the correct direction and ending at the correct hemifield were classified as correct. A saccade that ended at the wrong hemifield was classified as an error, and a saccade that started in the wrong direction, but ended at the correct hemifield was classified as a turn-around saccade (TAS). In TAS, the turn point was calculated by taking the point with the maximum x-value after which the trajectory changed direction, the latency of this turn point was calculated as the time at which horizontal direction changed, with respect to the target onset time.

INSERT FIGURE 1 HERE

Results & Discussion

The eye movement trajectories of one of the participants split by the four conditions are shown in Figure 1 for illustrative purposes. In the crossed hands posture, immediate response condition revealed more turn-around saccades (TAS; 5.13%) than the rest of conditions (<0.40%; see Figure 2b). This was precisely the condition revealing longer onset latencies for correct saccades and more initial errors (see Figure 2a). To test this statistically, we performed a repeated-measures ANOVA on the saccade onset latencies for correct straight saccades with the factors response mode (immediate vs. delayed) and posture (crossed vs. uncrossed arms). We found a main effect for posture (F(1,7)=10.03, p<.05) and an interaction between posture and response mode (F(1,7)=16.41, p<.01), indicating a slow down in latency for crossed-hands posture in the immediate response condition only ($t_{df=7}$=4.02, p<.01; no significant difference in the delayed condition: $t_{df=7}$=0.26, p=.81). In terms of initial error rate, a repeated-measures ANOVA returned a main effect for posture (F(1,7)=11.76, p<.05), a main effect for response mode (F(1,7)=7.63, p<.05) and an interaction between these two (F(1,7)=9.96, p<.05). This pattern was analogous to the latency analysis (see Figure 2b).

INSERT FIGURE 2 HERE

Despite the low number of TAS (an average of about 5 per participant as opposed to about 95 straight saccades), we further investigated the timing of TAS in this condition, in relation to the straight saccade onsets. In particular, we analysed onset latency for TAS and straight saccades separately, within the immediate response arms crossed condition. TAS were initiated faster (248±24 ms) than the straight saccades in the crossed condition (319±25 ms; $t_{df=5}=4.38$, $p<.01$)[1], but equivalent to the straight saccades in the uncrossed posture (227±13 $t_{df=5}=.94$, $p=.39$). Indeed, the mean onset latency of straight saccades was on average 92 ms slower for the crossed than for the uncrossed arm position ($t_{df=7}=4.18$, $p<.01$). Remarkably, we also found that the time at which the turn point took place (332 ± 30 ms) in the TAS was similar to the mean onset latency of straight saccades in the crossed hands posture (319 ± 25 ms; $t_{df=5}=1.77$, $p=.14$).

Although erroneous saccades (ending in the wrong hemifield) were uncommon (<2%), we calculated their mean onset latencies (384 ± 123 ms, 290 ± 34 ms and 445 ± 138 ms for uncrossed and delay, crossed and immediate, and crossed and delayed conditions respectively; in the uncrossed immediate condition no errors were made). The latencies of erroneous saccades are not significantly different from

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[1] Two participants did not make TAS, and therefore we excluded this data from the analysis in which we compared TAS to other conditions (and therefore there are less degrees of freedom in those comparisons).

the onset latencies of either straight-and-correct saccades or TAS in all three conditions in which errors were present (all p>.26).

Taken together, the results suggest that immediate somatosensory saccades in the crossed arm condition were frequently postponed to be able to make a correct and straight response. When a saccade was initiated earlier in time, it was likely to start off in the wrong direction and had to be corrected in-flight, resulting in a TAS. Interestingly, these TAS started at the same moment in time as the saccades executed if the arms were uncrossed, and they turned around at about the same moment in time as correct straight saccades started when the arms were crossed. This pattern is suggestive of the relative timings corresponding to the process of tactile remapping, whereby different representations of the tactile event in space are available at different times. Here, the participant either ‘waits’ until the remapping is completed (thus, adding a constant to the overall RT) or initiates the saccade using the early somatotopic/anatomical representation of touch and then corrects the direction online when the information in terms of external coordinates is available later on (i.e., remapping process is completed). In Experiment 2 we sought for replicability of this pattern, and to test our hypothesis by checking if a speed up in saccadic RTs would increase the proportion of TAS.

Experiment 2

If TAS critically depend on whether remapping has not yet been completed by the time the saccade is initiated, we expect to find an increase in TAS when average onset latencies are shorter. We therefore altered the experimental procedure to induce faster saccades by introducing a gap between the offset of the fixation dot and the tactile stimulus. This procedure, often referred to as gap-paradigm, has been shown to produce faster reaction times in visual experiments (e.g. Gezeck, Fischer, & Timmer, 1997; Gomez, Athena, Lopez-Mendoza, Gomez, & Vazquez, 1995; Kingstone & Klein, 1993). Moreover, we also increased the perceived strength of the tactile stimulus, which has been shown to elicit faster reaction times too (Post & Chapman, 1991).

Method

Participants, Design and Procedure

Twenty new participants from the same pool as the previous experiment (13 female; 17 right-handed; mean age 25.6, range 18-38) took part in this experiment. The procedure and the experimental setup were exactly the same as in Experiment 1 except for the following: we introduced a 200 ms gap between the disappearance of the fixation dot and the onset of the tactile stimulus. Moreover, the tactile stimulus now consisted of a burst of 3 consecutive 2 ms taps within a 15 ms period. The sample rate of the eye tracker in this experiment was increased to 500 Hz. We now used only an immediate response mode, and measured 4 blocks of 50 trials, two with crossed-hands and two with uncrossed hands posture (order ABAB or BABA counterbalanced over participants).

Analysis

The analysis was similar to experiment 1. After allocation of the saccades we retained 91% of the original trials. Data from one participant were discarded because of the high prevalence of invalid saccades (failure to make any eye movement or to start at the fixation cross).

INSERT FIGURE 3 HERE

Results & Discussion

Saccade trajectories of one of the participants for uncrossed and crossed hands are shown in Figure 3 for illustrative purposes. As expected, the number of TAS in the crossed hands condition increased as compared to experiment 1 (5.13% in experiment 1, 12.30% in experiment 2; $t_{df=21.8}$=2.22, p<.05). Error rate was 0.90%, 5.70%, for uncrossed and crossed hands respectively (see Figure 4).

We compared the mean onset latencies for experiment 1 (270 ± 16 ms, immediate conditions only) and experiment 2 (219 ± 13 ms) with a univariate ANOVA with experiment and hand posture as the main factors. We found a main effect for experiment (F(1,52)=7.87, p<.01), confirming that our modified experimental procedure indeed yielded faster onset latencies in experiment 2. We also found a main effect of hand posture (F(1,52)=14.16, p<.001) indicating again faster onset latencies for the uncrossed hands posture. For an overview of the timings in the different conditions of experiment 1 and 2, see Figure 5.

Similar to experiment 1, TAS in the crossed hands posture were initiated faster (194 ± 14 ms) than the straight saccades in the same posture (248 ± 16 ms; $t_{df=18}$=4.75, p<.001)[2], and equivalent to the latency of straight saccades in the uncrossed hands posture (194 ± 11 ms; $t_{df=18}$=0.54, p=.59). In fact, the mean onset

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[2] One participant did not make any TAS therefore we excluded them from the analysis in which we compared TAS to other conditions (and therefore there were less degree of freedom in those comparisons).

latency of straight saccades was longer for crossed than for uncrossed arm arm posture ($t_{df=19}$=5.54, p<.001). The time at which the turn of the TAS took place (279 ± 21 ms), was slightly higher compared to the mean onset latency of straight saccades in the crossed hands posture (248 ± 16 ms;$t_{df=18}$=3.29, p<.05).

Mean onset latencies for errors (saccades ending at the wrong side) were 257 ± 46 ms and 237 ± 33 ms for uncrossed and crossed conditions respectively. The onset latencies for errors were neither significantly different from the TAS (194 ± 14 ms; $t_{df=12}$=.44, p=.67) nor from the straight saccades (248 ± 16 ms; $t_{df=13}$=1.10, p=.29) under crossed conditions.

INSERT FIGURE 4 HERE

Note that the times reported here are absolute RTs, in the sense that in addition to the process of interest, they also include the various stages necessary for a saccadic reaction such as sensory processing time and motor delays, which are timings subject to change from one paradigm to another (Thompson, Hanes, Bichot, & Schall, 1996). The particular difference in absolute RTs from Experiment 1 and 2, we believe, is caused by a combination of both components: shorter sensory processing and motor delay due to the use of stronger stimulation and the gap paradigm (respectively) in Experiment 2. Remarkably, this speed up in the average onset latencies for correct saccades from Experiment 1 to Experiment 2 (with the hands crossed; $t_{df=13.28}$=2.38, p<.05), was not accompanied by quicker onset latencies for TAS in experiment 2 as compared to experiment 1 ($t_{df=8.85}$=1.91, p=.09). This reflects that the distribution of

RTs did not shift uniformly, but instead, that more saccades accumulated on the quick tail of the distribution leading to the increase in TAS frequency, as predicted. In fact, there was no difference in the time of the turn point of TAS between experiments ($t_{df=10.39}$=1.42, p=.18), just as predicted if TAS latency in particular depended on the availability of tactile remapping information. What is more, the assumption that tactile remapping takes place at about the same time after *stimulus* onset and thus, it is equivalent in the crossed-arms posture of experiment 1 and 2, is further supported by the preservation, across experiments, of the relative timing in the turn-around point in TAS with respect to saccade onset time (as shown in the analyses above). The difference between onset time and turn-around time in TAS is 84 ± 10 ms in experiment 1, and 85 ± 10 ms in experiment 2 (not significantly different).

INSERT FIGURE 5 HERE

General Discussion

This study addressed the time course of tactile remapping from a somatotopic to a spatial reference frame. To do so, we measured eye movement timings and trajectories towards tactile targets on the hands in either a crossed or an uncrossed arm posture. Note that remapping is probably less computationally demanding in the "default" uncrossed posture (see Melzack & Bromage, 1973; Bromage & Melzack, 1974), where both anatomical and external reference frames are aligned. Instead, when the hands are crossed, there is a conflict between external and anatomical representations. As suggested by previous research, the external spatial representation of touch changes through time (Azañón, Camacho, & Soto Faraco, 2010; Azañón & Soto-Faraco, 2008a, 2008b). Thus, the difference in saccade onset time between uncrossed and crossed arm posture can inform us about the extra time that it takes to resolve the conflict in the tactile remapping process. In both experiments we found that saccades in the crossed arm condition were postponed in time, with respect to uncrossed arms, to be able to make a correct and straight response to the target. Interestingly, when saccades started early, then they often started toward the incorrect (but anatomically congruent) side and an in-flight correction was required, resulting in a turn-around saccade. These TAS started on average at about the same latencies as the saccade onsets with uncrossed arms, and the correction took place at about the same time as the onset of straight saccades with crossed-arms. This pattern was replicated in two experiments, with different absolute RTs, and is suggestive of the timings corresponding to the process of tactile remapping, whereby different representations of the tactile event in space are available at different times. Here, the participant either ‘holds on’ until the remapping is completed (thus, adding a constant to the overall RT) or initiates the saccade using the somatotopic/anatomical representation of touch and then corrects the direction online when the information in terms of external coordinates is available (when remapping is completed). Note that when saccades were delayed by instruction (Experiment 1), none of these effects were found. Therefore, we can attribute the variability observed in immediate saccades to online processes occurring by the time the saccades were planned and executed.

Both the mean saccade onset latency of correct and straight saccades and the turn point of TAS in the crossed hands posture are an indication of the time it takes to integrate tactile input with proprioceptive information, presumably necessary for tactile remapping. We found that tactile remapping should be completed 319 ms after target onset in experiment 1 and 248 ms after target onset in experiment 2 (saccade onset for straight saccades in crossed immediate conditions). This is in accordance with earlier research; Yamamoto and Kitazawa (2001) suggested that it might take around 300 ms to complete the process of remapping from somatotopic into spatial coordinates.

However, it is important to note that our estimate is based on both the time that it takes to remap plus some constant delays related to sensory processing of the tactile stimulus and the motor delay to initiate an eye movement, as suggested in the results and discussion section of experiment 2. We therefore suggest that these timings provide an upper bound estimate of the time it takes for tactile remapping to complete. It is difficult to provide a precise estimate of the motor delays in a task, because it is the time elapsed between a decision has been made, and the effective movement of the eye. According to research in monkeys (Thompson, Bichot, & Schall, 1997; Thompson, et al., 1996) the motor delays in a visual discrimination task can range from 38 ms to 77 ms, which was assessed as the time elapsed between the moment the frontal eye fields (FEF) neurons provided discriminative signal about the target, and the onset of the movement of the eye. In monkeys, this motor delay was a good predictor of the total saccade latency, and varied with task-related factors. If we were to assume that motor delay was proportional to our saccade latencies and apply the 3/5 rule to estimate human neural timings from those of monkey (Schroeder, Mehta, & Givre, 1998), one could estimate that motor delay could range between 63-128 ms in the present data. A delay around this magnitude should be subtracted from the absolute timings resulting in Experiments 1 and 2 in order to reveal the actual moment at which remapping is complete.

As we discussed in the introduction, Heed and Röder (2010) found that limb position can modulate attentional effects as early as 100-140 ms. We could consider that by this latency, remapping must have been *started* (i.e., it would be a rough upper-bound estimate of the time remapping begins). Azañon and Soto-Faraco (2008a) found that around 360 ms remapping must have been *completed*, which according to Kitazawa (Kitazawa, 2002; Yamamoto & Kitazawa, 2001) should already been completed around 300 ms. Our finding of 248-319 ms is an upper-bound estimate of *completion* of remapping and is comparable to these previous results. If we speculate about the motor delay from monkey research data (on average, 95ms), then from our saccadic onset data (average across experiments 284 ms) we could approximate an estimated completion time of around 190 ms.

Our paradigm could be seen as a decision making problem, and therefore the data obtained could be described with a model whereby noisy evidence for a decision is accumulated over time until a criterion level, which determines the initial decision, is reached. Information that is still in the pipeline at that moment is processed to subsequently reverse or reaffirm the initial decision. Resulaj, Kiani, Wolpert and Shadlen (2009) have modelled a similar decision making problem for hand movements and found that hand movements toward a target sometimes betrayed a change of mind, i.e. they found *curved* hand movement trajectories towards a target that was either on the left or the right side opposite to the start position. These previous findings are in line with our current results and at first sight Resulaj et al.'s model might as well offer a possible framework for the present data. In our study, in the crossed hand condition, the two reference frames (external and internal) can be understood as competing sources of information, which come available in different time frames.

In sum, we used eye movements as a measure to investigate the timing of the integration of touch and proprioception (tactile remapping). We found that participants rather postpone their saccade initiation until tactile remapping is completed. If they do initiate earlier in time, they are likely to initiate the saccade towards the anatomical side and then correct it online. We found that tactile remapping must be completed around 250-320 ms after stimulus presentation, minus the time it takes for motor planning and execution of a saccade (estimated at around 60-130 ms).

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Figure Captions

Figure 1. Eye movement trajectories of one of the participants for the four different conditions of experiment 1. All saccades directed to a stimulus on the right side were mirrored for clarity.

Figure 2. (A) Saccade onset latency plotted against initial saccade angle for the four different conditions of experiment 1 (for all participants). All saccades directed to a stimulus on the right side were mirrored, resulting in positive angles for the correct direction and negative angles for the incorrect angles. (B) Proportion of errors and turn-around saccades for the four different conditions of experiment 1 (averaged over participants; error bars represent standard error of the mean).

Figure 3. Eye movement trajectories of one of the participants for the two different conditions of experiment 2. All saccades directed to a stimulus on the right side were mirrored for clarity.

Figure 4. (A) Saccade onset latency plotted against initial saccade angle for the two different conditions of experiment 2 (for all participants). All saccades directed to a stimulus on the right side were mirrored, resulting in positive angles for the correct direction and negative angles for the incorrect angles. (B) Proportion of errors and turn-around saccades for the four different conditions of experiment 2 (averaged over participants; error bars represent standard error of the mean).

Figure 5. Summary of the reaction times of the critical conditions in both experiments. (Averaged over participants; error bars represent the standard error of the mean).

Figure 1

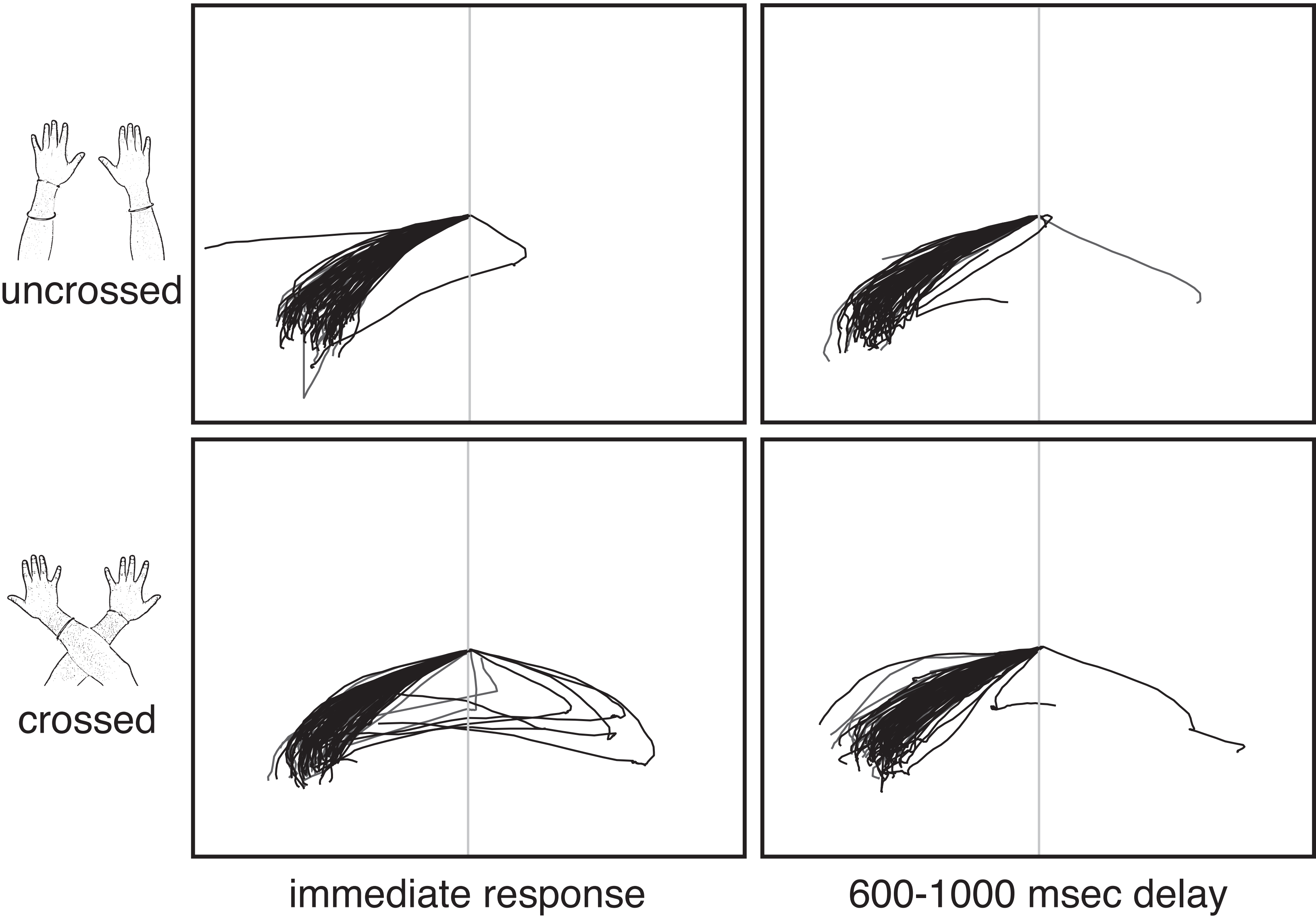
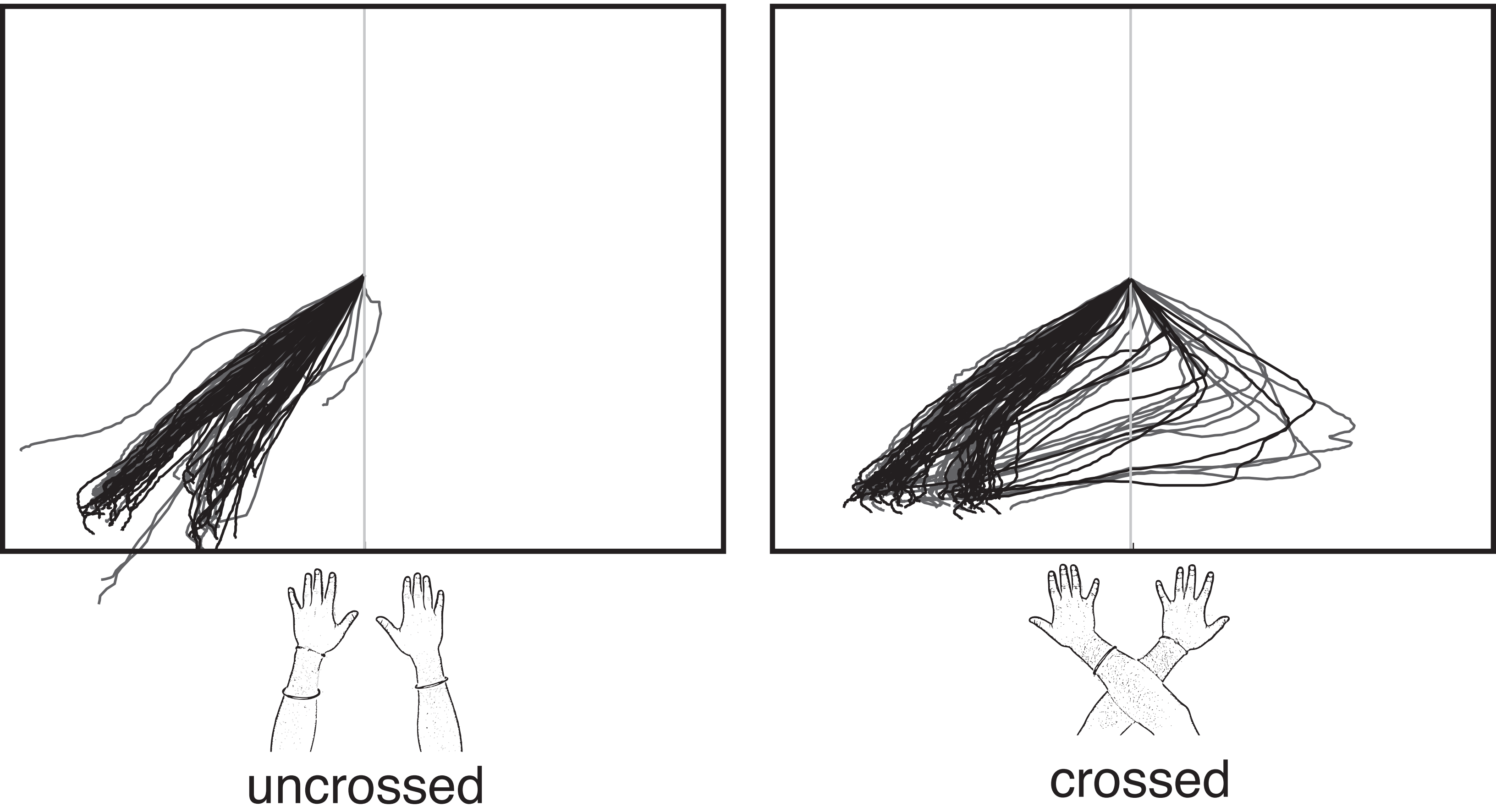


Figure 3



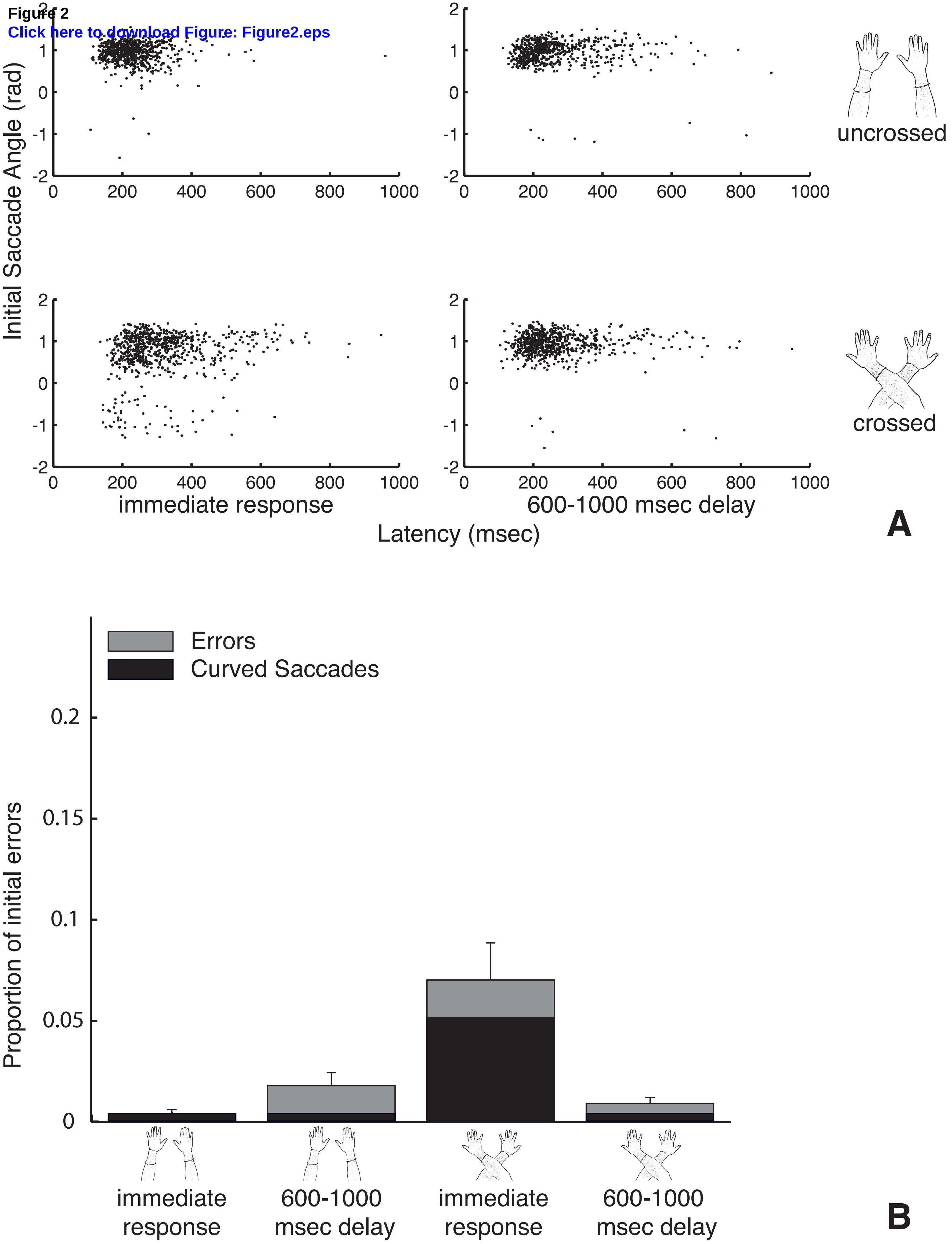

Initial Saccade Angle (rad)
2
1
0
-1
-2
0
200
400
600
800
1000
uncrossed
crossed
immediate response
600-1000 msec delay
Latency (msec)
A
Errors
Curved Saccades
Proportion of initial errors
0.2
0.15
0.1
0.05
0
immediate response
600-1000 msec delay
immediate response
600-1000 msec delay
B

Figure 4

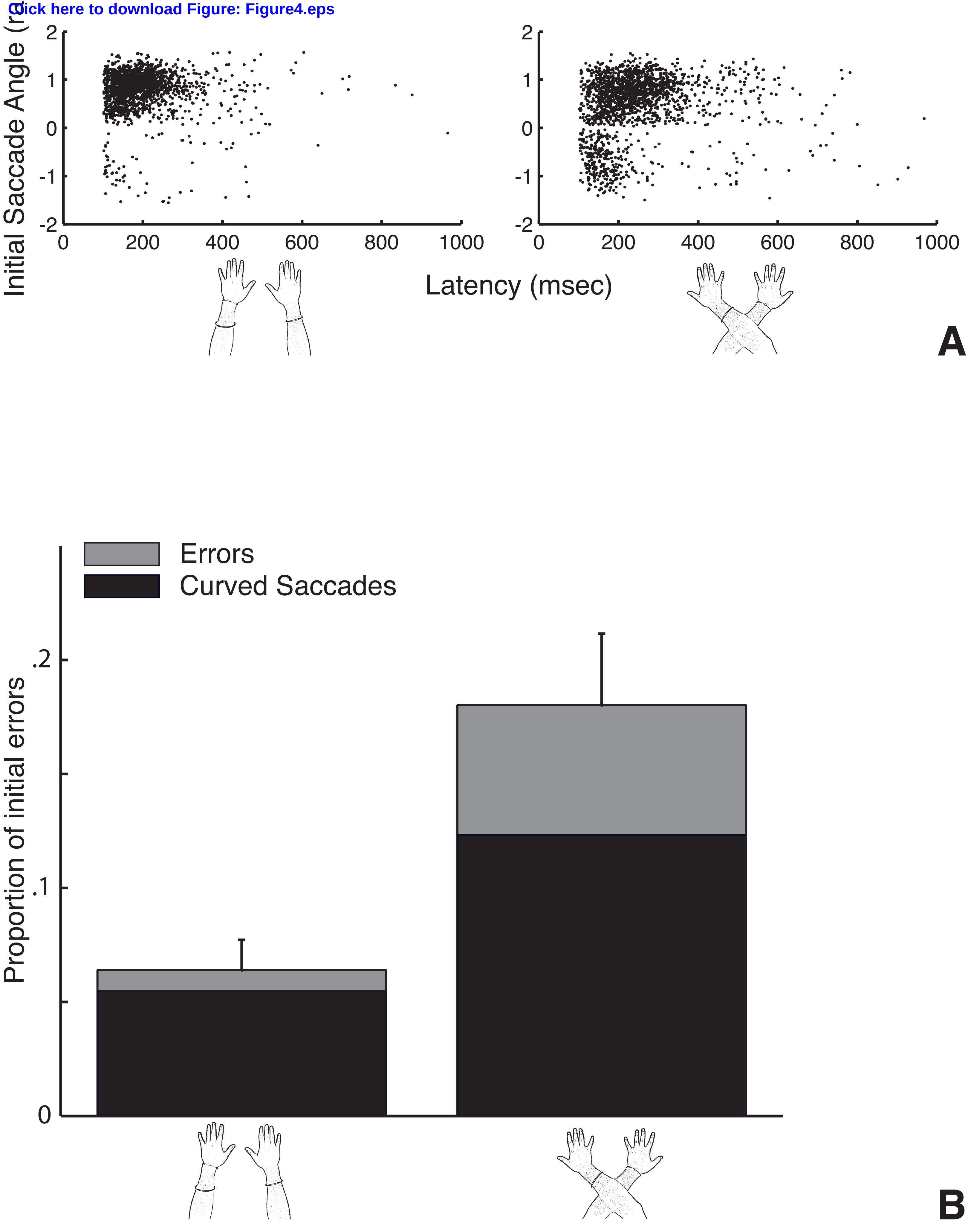

Initial Saccade Angle (rad)
2
1
0
-1
-2
0
200
400
600
800
1000
Latency (msec)
A
Errors
Curved Saccades
Proportion of initial errors
.2
.1
0
B

Figure 5

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