Report

A Soft Handoff of Attention between Cerebral Hemispheres

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Summary

Each cerebral hemisphere initially processes one half of the visual world. How are moving objects seamlessly tracked when they traverse visual hemifields? Covert tracking of lateralized objects evokes a difference between slow-wave electrophysiological activity observed from contralateral and ipsilateral electrodes in occipitoparietal regions. This event-related potentials (ERP) waveform, known as contralateral delay activity (CDA) [1, 2], is sensitive to the number of objects tracked [1, 2] and responds dynamically to changes in this quantity [3]. When a tracked object crosses the midline, an inversion in CDA polarity revealed the dropping of the object's representation by one hemisphere and its acquisition by the other. Importantly, our data suggest that the initially tracking hemisphere continues to represent the object for a period after that object crosses the midline. Meanwhile, the receiving hemisphere begins to represent the object before the object crosses the midline, leading to a period in which the object is represented by both hemispheres. Further, this overlap in representation is reduced if the midline crossing is unpredictable. Thus, this process is sensitive to observer expectations and does not simply reflect overlapping receptive fields near the midline.

Results and Discussion

We recorded event-related potentials (ERPs) from healthy young adults as they covertly tracked a vertically or horizontally moving object while holding central fixation (see the Supplemental Results and Discussion available online for additional information on eye movements). As shown in Figure 1A, on each trial, a pair of objects was presented in each quadrant. A brief (500 ms) cue informed the observer which object to track. ERP waveforms were time-locked to the onset of this cue. When the cue disappeared, all objects began to move either clockwise or counterclockwise, taking each pair over either the horizontal or vertical midline. Movement toward midlines was held constant so that all objects crossed their respective midline at the same time. Movement in the orthogonal direction was less constrained. For example, as a pair of objects moved to the right, they would vacilate up and down, allowing their paths to cross and making tracking difficult (see the Supplemental Results and Discussion and Figures

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S1 and S2). As the objects were otherwise identical, close attention was required in order to track the target. Objects moved for 2.55 s, crossing the midline 1.70 s after cue onset (1.20 s after motion onset). This design ensured that the number of objects in each visual hemifield was always balanced and the distance traveled by objects on vertical and horizontal trials was identical. For more information on experimental procedures and behavioral data, see the Supplemental Information.

Each trial was categorized in terms of the whether the tracked object crossed the vertical or the horizontal midline. We averaged across five pairs of occipitoparietal electrodes (selected based on prior work [1, 4]) and categorized the two resultant waveforms as contra- or ipsilateral with respect to the initial position of the tracked object (see Figure 1B). To simplify analysis, we collapsed across direction of motion and initial position. Only correct trials with no eye movements or blinks artifacts were included. In our analyses, we refer to activity over the initially contralateral hemisphere as the *source hemisphere activity* and activity from the initially ipsilateral hemisphere as *target hemisphere activity*. (Note that this naming convention is specific to the horizontal condition: in the vertical condition, the target hemisphere never receives the object information since it was confined to a single visual hemifield.)

On vertical trials, when the tracked object was *not* switching hemispheres, we observed a large contralateral delay activity (CDA) in the time window before the attended object crossed the horizontal meridian (800–1,200 ms: t(13) = 7.76, p < 0.001) and a similar CDA after the crossing (2,000–2,400 ms: t(13) = 7.35, p < 0.001). There were no differences between those time periods (t(13) = 1.64, p = 0.123). In contrast, on horizontal trials when the attended objects crossed the vertical midline and moved from one visual field to the other, we observed a large CDA prior to the crossing (800–1,200: t(13) = 11.03, p < 0.001). The waveform then inverted in polarity shortly after the tracked object crossed the vertical meridian, such that ipsilateral activity was more negative than contralateral activity (2,000–2,400 ms: t(13) = −3.54, p = 0.004). As predicted, activity from the hemisphere contralateral to the *current* location of the tracked object was more negative than ipsilateral activity regardless of whether the tracked object stayed within a hemifield or crossed between fields, revealing a dynamic remapping of attended object information between hemispheres.

Like the handoff between cellular phone towers transferring a live call on a moving mobile device, the handoff between hemispheres can be decomposed into two events that could occur at different times. There is a moment when the target hemisphere picks up the attended object information and another when the source hemisphere drops the information. This hemispheric handoff is analogous to presaccadic remapping [5, 6], where two findings are consistent across a range of methodologies [7–10]. First, target information is typically picked up *prospectively*, meaning that cells at the new, postsaccadic position represent the object before the completion of the saccade [7]. Second, the remapping closely approximates a "hard handoff" in which the cells that code the object in its original eye position quickly truncate their activity once
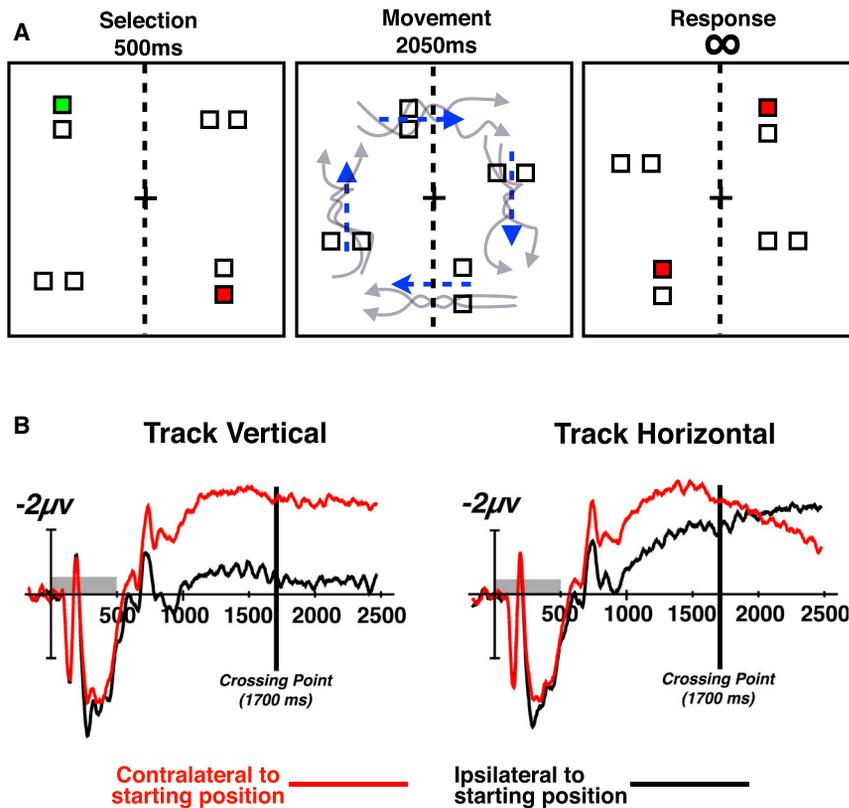
Figure 1. Experimental Paradigm and Contralateral Waveforms for Experiment 1

(A) Schematic illustration of experiment 1 paradigm. Dotted lines and light gray lines were not visible in the experiment.

(B) Vertical and horizontal ERP waveforms broken down by object movement type. Note that negative is plotted up here and throughout the paper.

See also Figure S1.

the new location begins to be represented, resulting in little temporal overlap between the activity of the two sets of neurons [11, 12].

To measure the pickup and release during the handoff of an attended item moving across the midline, we compared activity from the source and target hemispheres as a function of movement type (horizontal versus vertical; Figure 2A). In this analysis, the vertical condition served as a baseline against which to compare the relative difference evoked as the attended object moved from source to target hemifields. As the two conditions were otherwise matched, we infer that any difference observed between the two is due to the handoff of object information between hemispheres. We determined when the vertical and horizontal trials began to differ for each hemisphere by sliding a 4 ms window backward in time from the end of the trial until at least ten successive time windows did not differ significantly at p = 0.001 (Figure 2B; see the Supplemental Results and Discussion for more details on analysis). This conservative analysis does not measure the time at which the handoff is first initiated, but instead provides an upper-bound estimate of the time by which the handoff has reliably occurred [13]. By this measure, the source hemisphere released object information at 2,372 ms (SD: 89 ms), or 672 ms after the attended object crossed the midline, having traveled 2.0° past the midline by that time. At this point, the source hemisphere showed a reduced negativity for horizontal trials relative to vertical trials, indicating the release of attended object information. Turning to pickup by the target hemisphere, divergence occurred at 1,292 ms (SD: 355 ms), roughly 400 ms (1.2°) *prior* to the attended object crossing the midline. Similar to saccadic remapping, the target hemisphere appears to prospectively pick up the incoming attended object well before it crosses the midline.

To examine the relative timing differences between pick up and release of attended object information, we used a bootstrapping procedure to determine whether the increase in target hemisphere activity became significant reliably before the decrease in source hemisphere activity. Specifically, we randomized condition labels (target or source) and then sampled with replacement as many waveform pairs as we had observers. We computed the difference between pickup and drop-off points for each bootstrapped data set and then repeated this procedure 10,000 times in order to create a sample distribution [14]. Z scores of the observed data relative to the bootstrap data served as a measure of the likelihood that the observed values occurred by chance. We found that the difference in target activity became significant reliably earlier than source activity (Z score = 4.05, p < 0.001). This is strong evidence that the target hemisphere began tracking the object prior to the source hemisphere releasing the object, resulting in ~1,000 ms when both hemispheres actively tracked the object during the exchange. In contrast to the hard handoff observed for saccadic-based remapping, which is characterized by the abrupt truncation of activity in the source hemisphere once the target hemisphere picks up the attended object, these data support a soft-handoff model in which both hemispheres share object information for an extended period of time.

It is important to note that our statistical approach focuses on the relative differences between the two conditions, rather than absolute time points. As such, it is not surprising that the estimated time when the object was dropped falls several hundred milliseconds after crossing the midline, although the waveform appears to differ from zero prior to this time point. More observers would almost certainly result in earlier time estimates. However, there is no reason to assume that the overall pattern of pickup occurring before drop-off would change with more observers.

The pickup-before-drop-off results of experiment 1 might reflect an anatomical constraint based on the overlap of receptive fields from the two hemispheres at the vertical midline [15]. Once an attended object comes within a certain distance of the vertical meridian, receptive fields in both hemispheres might passively monitor the attended object without any need for active coordination. Experiment 2 tested this hypothesis by manipulating the predictability of the attended object crossing the vertical or horizontal meridian. If the handoff reflects receptive field overlap around the midline, only the physical position

A

Source Hemisphere

Target Hemisphere

-2μv

-2μv

500 1000 1500 2000 2500

500 1000 1500 2000 2500

Crossing Point (1700 ms)

Crossing Point (1700 ms)
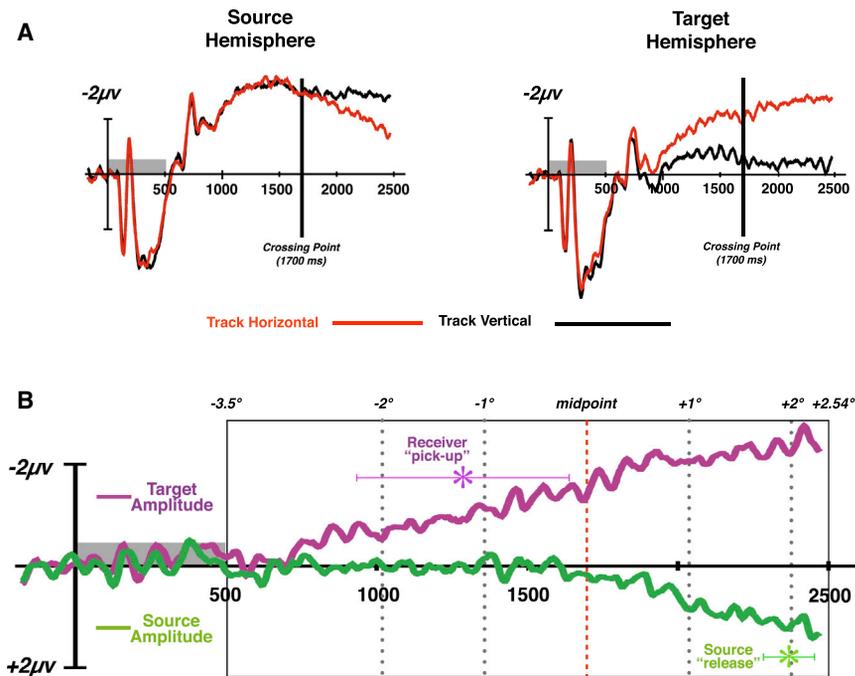
Track Horizontal   Track Vertical

Figure 2. Source and Target Hemisphere Waveforms for Experiment 1

(A) Waveforms from the source and target hemispheres. These data are replotted from Figure 1B to emphasize hemisphere rather than object motion.

(B) Difference waveforms for the target and source hemispheres. Asterisks denote the point in time when the waveform reliably differed from zero for at least ten successive time windows for the first time. Error bars represent the SD. See also Figure S2.

B

-3.5°   -2°   -1°   midpoint   +1°   +2° +2.54°

-2μv

Target Amplitude

Receiver "pick-up"

*

500   1000   1500   2500

Source Amplitude

Source "release"

+2μv

of the object relative to the midline should affect handoff time. However, if the handoff reflects active coordination between the hemispheres, we might expect contextual factors such as predictability to come into play. In experiment 1, midline crossing was highly predictable, allowing the target hemisphere to prepare for the crossing in advance. If the crossing were less predictable, the handoff might be delayed. The *predictable* block of experiment 2 replicated experiment 1. Initial object motion was perfectly predictive of the final hemifield position. In the *unpredictable* block, on 50% of trials, all objects reversed trajectory back toward their starting position when they reached the vertical or horizontal midline (see Figure 3A). These trials were randomly interleaved with trials where the objects did not reverse directions thus making the movement in this block of the experiment more unpredictable than in the first block. For present purposes, we focused on trials in the unpredictable block that did not reverse trajectories. These trials were visually identical to the trials in the predictable block; they differed only in context. In order to assess the timing of the interhemispheric cooperation and focus on the unique impact that an attended object switching hemifields had on the waveforms, we again subtracted horizontal activity from matched vertical. For additional details and analysis on reversed trajectory trials, see the Supplemental Results and Discussion.

The predictable block of experiment 2 replicated the basic effect from experiment 1: horizontal and vertical activity diverged *after* the attended object crossed the midline for the source hemisphere (2,381 ms; SD: 141 ms, 2.9° past midline) and *before* the attended object crossed the midline for the target hemisphere (1,222 ms; SD: 158 ms; 0.9° prior to midline; see Figure 3B). In the unpredictable block, the source hemisphere released object information at roughly the same relative time as in the predictable block (2,168 ms; SD: 293 ms; 2.2° past midline; see Figure 3C). However, the target hemisphere picked up the attended object information much later when the object's motion was unpredictable than when it was predictable. In the unpredictable block, by

our conservative timing measure, the tracked object was picked up after an average 2,068 ms (SD: 315 ms, 1.9° *past* midline). Our simple manipulation of motion predictability led to approximately an 800 ms delay in remapping the attended object to the target hemisphere (Z score = 2.58, p = 0.010). In contrast, the source hemisphere was unaffected: activity in this hemisphere continued to represent attended object information after it crossed the midline for an equivalent duration in both cases (Z score = 0.56, p = 0.576; for converging evidence, see the Supplemental Results and Discussion and Figure S3). Further, while pickup time was significantly earlier than release time in the predictable condition (Z score = 3.5; p < 0.001), it was not significantly different in the unpredictable condition (Z score = 0.50; p = 0.617). If the shared object representation in experiment 1 reflected source and target hemispheres both representing a strip of the visual field straddling the midline, then motion predictability should not have influenced the time course of the handoff. Thus, while proximity to the midline certainly has an influence on object representation, we argue that the handoff is not an entirely hardwired consequence of receptive field overlap at the midline. For converging evidence that context influences the timing of the handoff using a fractional area latency measure, see the Supplemental Results and Discussion.

These experiments reveal three core properties of the remapping process between hemispheres during covert attentional tracking of objects that travel between visual hemifields. First, similar to saccadic remapping, we find that remapping for predictable movement occurs *prospectively*, with the target hemisphere beginning to represent the attended object at least 300 ms prior to the object crossing the midline. These results echo those of Assad and Maunsell [16], who found that the spiking rate of neurons in the posterior parietal cortex increased 20–120 ms prior to the predictable occlusion of a tracked object. Second, our data suggest that attentional remapping approximates a soft handoff in which the source hemisphere holds on to object activity after the target hemisphere begins to represents the object, and well after the object has crossed the midline. This finding is broadly similar to the recent observation that unit activity for a newly attended object increases prior to the decrease in activity for the previously attended object [17]. Third, the nature of interhemispheric cooperation is context dependent. If the midline crossing is unpredictable, the target hemisphere does not reliably pick up object information until after the object crosses the midline. Thus, predictable object movement leads to a
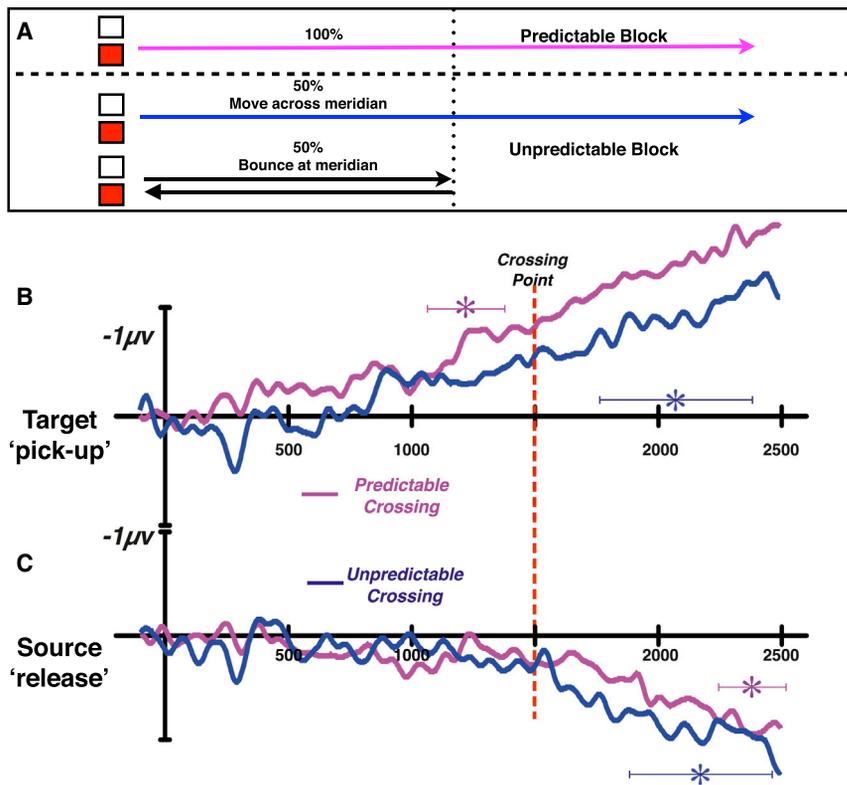
Figure 3. Experiment 2 Trial Schematic and Difference Waveforms

(A) Schematic for horizontal trial movement in experiment 2. Vertical trials followed the same pattern.

(B) Difference waveforms for experiment 2. Unpredictable data are taken from the 50% of trials in which the objects crossed the midline. Asterisks denote the point in time when the waveform reliably differed from zero for at least ten successive time windows for the first time. Error bars represent the SD.

See also Figure S3.

longer period of time when the two hemispheres appear to simultaneously represent object information.

We speculate that remapping is not specific to transsaccadic perception, but rather is a general property of the visual processing system. We often need to keep track of objects that we are not directly fixating. When a covertly attended object (such as a car in a rearview mirror) travels from one visual hemifield to another, it is necessary for object information to be sent from one cortical hemisphere to the other. The present results provide important initial steps toward characterizing how dynamic cooperation between the two hemispheres allows this computationally complex handoff to be completed. Perception of a stable visual world despite continuous changes to retinal inputs is a fundamental problem in cognitive neuroscience. The current work reveals that this stability involves complex cooperation between the two hemispheres to allow dynamic remapping of attended object representations. This interaction is sensitive to the predictability of object motion, with greater predictability producing more prospective tracking by the target cerebral hemisphere. The collaboration between the hemispheres may be responsible for stitching together the perceived visual world across two halves of the brain, and the paradigm outlined here is a promising method for studying this process.

Supplemental Information

Supplemental Information includes three figures, Supplemental Experimental Procedures, and Supplemental Results and Discussion and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.03.054.

Acknowledgments

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