Citation: Sambo, C.F. & Forster, B. (2011). When far is near: ERP correlates of crossmodal spatial interactions between tactile and mirror-reflected visual stimuli. NEUROSCIENCE LETTERS, 500(1), pp. 10-15. doi: 10.1016/j.neulet.2011.05.233

***Research Highlights**

- Visual and tactile stimuli are better integrated by the brain when they are spatially congruent
- Such spatial congruence effect occurs when visual stimuli appear in near but not in far space
- This effect is also present when visual stimuli are viewed through a mirror, *appearing* in far space
- We conclude that visual stimuli reflected in a mirror may be remapped as close to the body

When Far Is Near: ERP Correlates of Crossmodal Spatial Interactions between Tactile and Mirror-Reflected Visual Stimuli

Chiara F. Sambo[1, 2] * and Bettina Forster[1]

1. Department of Psychology, City University London
2. Department of Neuroscience, Physiology, Pharmacology, University College London

*Correspondence:
City University,
Northampton Square,
London EC1V 0HB (UK)
Email: chiara.sambo.2@city.ac.uk
Tel: +44 (0) 20 7040 0125
Fax: +44 (0) 20 7040 8185

Abstract

Visuo-tactile integration occurs in a privileged way in peripersonal space, namely when visual and tactile stimuli are in spatial proximity. Here, we investigated whether crossmodal spatial effects (i.e. stronger crossmodal interactions for spatially congruent compared to incongruent visual and tactile stimuli) are also present when visual stimuli presented near the body are indirectly viewed in a mirror, thus appearing in *far* space. Participants had to attend to one of their hands throughout a block of stimuli in order to detect infrequent tactile target stimuli at that hand while ignoring tactile targets at the unattended hand, all tactile non-target stimuli, and any visual stimuli. Visual stimuli were presented simultaneously with tactile stimuli, in the same (congruent) or opposite (incongruent) hemispace with respect to the tactile stimuli. In one group of participants the visual stimuli were delivered near the participants' hands and were observed as indirect mirror reflections ('mirror' condition), while in the other group these were presented at a distance from the hands ('far' condition). The main finding was that crossmodal spatial modulations of ERPs recorded over and close to somatosensory cortex were present in the 'mirror' condition but not the 'far' condition. That is, ERPs were enhanced in response to tactile stimuli coupled with spatially congruent versus incongruent visual stimuli when the latter were viewed through a mirror. These effects emerged around 190 ms after stimuli onset, and were modulated by the focus of spatial attention. These results provide evidence that visual stimuli observed in far space via a mirror are coded as near-the-body stimuli according to their *known* rather than to their *perceived* location. This suggests that crossmodal interactions between vision and touch may be modulated by previous knowledge of reflecting surfaces (i.e. top-down processing).

Keywords: Event-Related Potentials; Mirror; Peripersonal space; Visuo-tactile.

Introduction

Peripersonal space is the portion of space surrounding the body, where we interact with (e.g. reach) objects in the environment (e.g. [22]). In everyday life, objects falling within peripersonal space are normally perceived through more than one sensory modality, such as vision and touch. Accordingly, neurophysiological research in animals has identified a network of cortical and subcortical brain areas, including the ventral premotor cortex, the posterior parietal cortex, the putamen, and the superior colliculus, that subserves the visuo-tactile representation of peripersonal space [1, 4, 5, 7]. Specifically, a number of these neurophysiological studies, as well as neuropsychological (see [13, 14] for reviews) and neuroimaging [18, 23] investigations in human participants have shown that crossmodal interactions between touch and vision are stronger for visual stimuli in close proximity to the body part touched (i.e. within few centimeters), while crossmodal effects diminish when visual stimuli appear in extra-personal space at a distance of 35 cm or more from the participant's hands. Taken together, these findings suggest that the visuo-tactile representation of peripersonal space may be neurally distinct from the representation of far extra-personal space (see [3]).

However, recent research in humans and animals suggests that the multimodal representation of the body and of peripersonal space is plastic and can be modulated to incorporate regions of extra-personal space that become reachable by means of tools (e.g. [10, 20]). Moreover, recent studies have suggested that visuo-tactile peripersonal space may be remapped to include mirror-reflected images of body parts (and the space around these), which appear in extra-personal space and thus project the retinal image of distant objects [19, 21]. Namely, these studies have shown that tactile stimuli can interact with visual stimuli that are observed at a distance via a mirror. For example, Maravita and colleagues [19] showed in a right-brain-damaged patient that detection of contralesional (left) touch was decreased by the presentation of a simultaneous, task-irrelevant visual stimulus near the ipsilesional hand (i.e. crossmodal extinction) when visual stimuli were observed indirectly as mirror-reflections compared to when these were presented in far space at a distance that produced a comparable retinal image as the mirror image. Similarly, using a crossmodal congruency task whereby participants had to judge the elevation of tactile stimuli delivered either to their index finger (up) or thumb (down) while ignoring visual distractors presented at congruent or incongruent locations to touch, Maravita et al. [21] showed that crossmodal interferences by visual distractors on tactile elevation discriminations were more effective when visual distractors presented near the hands were observed via a mirror compared to conditions in which the visual distractors were presented at a distance from the hands. Furthermore, Helbig and Ernst [9] investigated visual-haptic interactions under direct-viewing and mirror-viewing conditions using a matching task in which a conflict between the seen and the felt shape of an object was created, and participants had to judge the shape of the object. These authors found a biasing effect of shape information from vision to touch and vice versa (i.e. visual-haptic interaction effects) irrespective of whether the object that the participants touched was viewed directly or through a mirror, although in the latter case visual and haptic stimuli were spatially separated.

Taken together, these results suggest that visuo-tactile interactions are stronger when visual stimuli presented near the hands are seen in a mirror compared to when these are presented in far space, and that such interactions in 'mirror' conditions are similar to those found under direct view of the hands and the visual stimuli in peripersonal space. This indicates that visual stimuli observed via a mirror are treated as near-the-body stimuli, according to their actual location (inferred by the knowledge of the properties of reflecting surfaces), rather than as distant stimuli as suggested by their retinal image (i.e. low-level physical processing). Thus, the findings above suggest that cognitive, top-down mechanisms rather than bottom-up processing may be involved in perceiving the location of visual stimuli observed via a mirror. However, the neural correlates of this process have not been hitherto addressed.

In a previous ERP study we showed that spatially congruent visual and tactile stimuli resulted in stronger crossmodal interactions compared to conditions in which the visual stimuli were presented at a different location in peripersonal or far space ([23]). Using a similar paradigm, here we investigated whether electrophysiological responses to tactile stimuli coupled with visual stimuli are modulated by the actual spatial relationship between tactile and visual stimuli when the latter are observed via a mirror ('mirror' condition). This condition was compared to the 'far' condition reported in Sambo and Forster ([23]), in which the visual stimuli were presented at a distance from the hands that produced a retinal image comparable to that in the 'mirror' condition.

We predicted that if mirror reflections of visual stimuli are treated as if they were distant objects in far extra-personal space (i.e. behind the mirror) as suggested by the retinal image that these project, no differences dependent on the spatial congruence of tactile and task-irrelevant visual stimuli would be present in ERP responses, similar to the condition in which visual stimuli are presented in far space ([23]). However, if mirror-reflected visual stimuli are coded as originating in peripersonal space, as previous neuropsychological and behavioural studies suggest (see above), ERPs in response to tactile stimuli would be modulated by the actual spatial relationship between visual and tactile stimuli. This would be reflected in an enhancement of ERPs in response to tactile stimuli presented with spatially congruent compared to incongruent visual stimuli, similar to what has been found for visual stimuli presented in peri-hand space and observed directly ([23]).

Methods

Participants

29 paid volunteers took part in the study while the data of five participants had to be excluded from further analysis due to an excess of alpha waves. Thus, 12 participants aged between 21 and 37 years (mean: 28.5) remained in the sample of the ‘mirror’ condition and 12 participants aged between 23 and 36 years (mean: 26.8) were included in the sample of the ‘far’ condition (the data of the latter condition was published previously in [23]). All participants were right-handed; and all had normal or corrected-to-normal vision by self-report. All participants gave their written informed consent. This study was performed in accordance with the Declaration of Helsinki (1964), and was approved by the Ethics Committee of City University London.

Apparatus and Procedure

Tactile stimuli and task-irrelevant visual stimuli were presented simultaneously on each trial, using the same apparatus and procedure used in [23]. Visual stimuli were presented with equal probability either in the same (congruent) or in the opposite (incongruent) hemispace with respect to the tactile stimuli. Participants performed a tactile discrimination task in which they had to respond to infrequent tactile target stimuli at the attended hand while ignoring tactile non-target stimuli and all visual stimuli (see [23] for details), in two experimental conditions: ‘mirror’ and ‘far’. As described in [23], in the ‘far’ condition the visual stimuli were always presented from the LEDs embedded in a set of two boxes located at a distance of 70 cm from the participants’ hands. In the ‘mirror’ condition, the visual stimuli were always presented from the LEDs embedded in a set of two boxes located close to the participants’ hands; however, the latter, and thus the visual stimuli, were hidden from the participants’ direct view by a wooden shield and could only be seen as indirect reflections in a mirror. The mirror (40 x 18 cm) was placed in front of the participants at the distance of 35 cm from their hands, and centred relative to the participants’ midline. Because of the properties of reflective surfaces, this resulted in the visual stimuli to appear at a distance of 70 cm from the participants’ hands; that is, double the distance between the LEDs and the mirror. Thus, the visual stimuli projected comparable retinal images in the two experimental conditions.

Recording and data Analysis

EEG (electroencephalogram) was recorded with Ag-AgCl electrodes from 28 scalp electrodes (midline electrodes: Fz, Fcz, Cz, Pz; electrodes over the right hemisphere: Fp2, F4, F8, Fc2, Fc6, C4, T8, Cp2, Cp6, P4, P8, O2 and the homologous electrode sites over the left hemisphere), using BrainVision recording system (BrainAmp amplifier and BrainVision Recorder software, version 1.02; Brain Products GmBH, Gilching, Germany; http://www.brainproducts.com). The amplifier bandpass was 0.01-100 Hz. Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ. EEG and EOG were sampled with a 500 Hz digitization rate, and subsequently were digitally filtered off-line with a 40 Hz low pass filter. EEG data were analyzed using BrainVision Analyzer software (version 1.05). EEG and EOG were epoched off-line into 700 ms periods, starting 100 ms before and ending 600 ms after the onset of tactile and visual stimuli. ERPs for tactile non-target stimuli coupled with task-irrelevant visual stimuli were averaged relative to a 100-ms pre-stimulus baseline. Trials with eye blinks (Fp1 or Fp2 exceeding ± 60 μV relative to baseline), horizontal movements (HEOG exceeding ± 30 μV relative to baseline) or other artifacts (a voltage exceeding ± 60 μV relative to baseline at electrodes Fc6, C4, Cp6, P4, P8, T8 and at homologous electrode sites over the left hemisphere) measured within 600 ms after stimuli onset, were excluded from analysis. Trials immediately following a response were also excluded from analysis in order to avoid contamination by movement-related artifacts (about 10% of the total trials on average). Electrodes were remapped to ipsilateral and contralateral recording sites with respect to the hand where the tactile stimulus was delivered.

On each trial simultaneous visual and tactile stimuli were presented and thus only bimodal ERPs were recorded. These were then compared for whether visual and tactile stimuli were spatially congruent or not. This paradigm allowed us to specifically investigate whether the spatial location of task-irrelevant visual stimuli in relation to the site of tactile stimulation modulates electrophysiological responses associated with processing within somatosensory cortex, under the assumption that any differences between bimodal ERPs in different experimental conditions are to be attributed to the different spatial relationship between visual and tactile stimuli (see [23] for a similar method). Thus, to investigate effects of crossmodal spatial congruence on processing within somatosensory cortex, ERPs recorded over and close to somatosensory cortex were compared for spatially ‘congruent’ and ‘incongruent’ trials, under ‘attended’ and ‘unattended’ conditions, for the ‘mirror’ and ‘far’ experimental conditions. ERP mean amplitudes were computed within the following measurement windows centred on the peak latencies of ERP components as revealed by peak detection analysis: P100 component (85-114 ms after stimuli onset), N140 component (115-190 ms), and N200 component (191-235 ms), and additionally for a later time window (236-300 ms). Statistical analysis (ANOVAs) was conducted on ERP mean voltage for electrode sites over and near somatosensory cortex contralateral to the tactile stimulus location (i.e. Fc5/6c, C3/4c, Cp5/6c, P3/4c, P7/8c, and T7/8c) where crossmodal spatial effects were expected based on previous evidence from single-cell recordings in animals (e.g. [4]) and neuroimaging and electrophysiological studies in humans (e.g. [16, 23]). Separate ANOVAs were conducted for each of the time intervals indicated above, and included the between-subjects factor Condition (‘mirror’ vs. ‘far’), and the within-subjects factors Congruence (‘congruent’ vs. ‘incongruent’), Attention (‘attended’ vs. ‘unattended’), and Electrode Site (see above).

Results

Figure 1 illustrates grand-averaged ERP waveforms elicited in the ‘mirror’ (*a*) and ‘far’ *(b)* conditions by tactile stimuli coupled with spatially congruent and incongruent visual stimuli under both attention conditions. For greater clarity, in Figure 1 *c* crossmodal effects are displayed together for the two experimental conditions collapsed across attended and unattended trials, at one of the electrodes (i.e. C3/4c; over somatosensory cortex). As can be seen from the figures, ERPs elicited in the 'mirror' condition show crossmodal spatial effects (defined as enhanced amplitudes for spatially congruent vs. incongruent visual and tactile stimuli) around 200 ms after stimuli onset, overlapping with the N200 component. These effects seem to be present specifically under attended trials. By contrast, no such crossmodal modulation is evident in the ERPs elicited in the 'far' condition, and furthermore the N200 component is not apparent in the ERPs elicited in this latter condition. In addition, in the N200 time range, as well as at later latencies, ERPs in the 'mirror' condition appear generally enhanced compared to ERPs in the 'far' condition.

Statistical analyses confirmed these preliminary observations. In the time range of the P100 component (85-114 ms after stimuli onset), no significant main effects or interactions between any of the factors were found. In the subsequent time interval, overlapping with the N140 component (115-190 ms after stimuli onset), a main effect of Attention was obtained ($F_{[1,22]} = 7.603$, $p < 0.02$), indicating that overall ERPs were enhanced for 'attended' compared to 'unattended' trials in this time interval. The interaction between Condition and Attention was not significant ($F < 1$, $p = 0.36$), indicating that in this time interval attentional effects in the two conditions did not differ significantly.

In the time interval of the N200 component (191-235 ms after stimuli onset), a main effect of the factor Condition was found ($F_{[1,22]} = 16.98$, $p < 0.001$), indicating enhanced amplitudes in the 'mirror' condition compared to the 'far' condition. A main effect of Attention was also obtained in this time interval ($F_{[1,22]} = 10.535$, $p < 0.005$), reflecting enhanced amplitudes for 'attended' compared to 'unattended' trials. Importantly, in the same time interval, a Condition x Congruence x Attention interaction was found ($F_{[1,22]} = 5.04$, $p < 0.04$) and two separate sets of analyses, one for the 'mirror' and one for the 'far' condition, were performed to explore this three-way interaction. In the 'mirror' condition, a significant Congruence x Attention interaction was obtained ($F_{[1,11]} = 8.16$, $p < 0.02$), indicating that crossmodal spatial effects were present for 'attended' but not for 'unattended' trials ($F_{[1,11]} = 7.60$, $p < 0.02$; and $F_{[1,11]} < 1$; $p = 0.28$, respectively). In contrast, the interaction between congruence and attention was not significant in the 'far' condition ($F < 1$, $p = 0.34$), suggesting that in this time interval such crossmodal effects were not present in this condition either for ‘attended’ or ‘unattended’ trials.

Finally, in the subsequent time range (236-300 ms after stimuli onset) a main effect of Condition ($F_{[1, 11]} = 17.50$, $p < 0.001$) and a main effect of Attention ($F_{[1, 11]} = 9.78$, $p < 0.01$) were found, indicating that in this time range ERPs were overall enhanced for the ‘mirror’ compared to the ‘far’ condition; as well as for ‘attended’ compared to ‘unattended’ trials irrespective of the experimental condition[1].

Fig. 1 *a, b, c* approximately here

Discussion

There is a substantial body of evidence showing that crossmodal interactions are stronger for spatially congruent compared to incongruent visual and tactile stimuli; that is, when visual stimuli are presented in peripersonal space near the stimulated body part (e.g. the hands) (see [11, 17] for reviews). Here, we provided neural (ERP) evidence that crossmodal spatial effects between vision and touch can also occur when visual stimuli presented in peripersonal space are observed indirectly in a mirror, although under this condition the retinal image is consistent with the visual stimuli being presented in far extra-personal space.

We found that ERPs recorded over and near somatosensory cortex were modulated by the spatial congruence of visual and tactile stimuli only in the ‘mirror’ condition; that is, ERP amplitudes were enhanced for tactile stimuli coupled with spatially congruent compared to incongruent visual stimuli in the ‘mirror’ condition, while no differences were observed in the ‘far’ condition. The crossmodal spatial effects in the ‘mirror’ condition were observed from around 190 ms after stimuli onset (i.e. overlapping with the N200 component) and were modulated by attention, in that such effects were present only when attention was directed to the site of tactile stimulation but not when attention was directed to the opposite side of space.

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[1] To rule out the possibility that visual evoked potentials (VEPs) generated by the *visual cortex* would be responsible for the ERP modulation by crossmodal spatial congruence at the electrodes of interest, we further tested whether ERPs recorded over visual cortex (i.e., at O1 and O2 electrodes) were modulated by the spatial location of visual stimuli in the ‘mirror’ condition (i.e. where crossmodal spatial effects were found) for the same time intervals and with the same factors used in the main analysis. No main effects or interactions involving any of the factors were found in any of the analysis time intervals (all $p > 0.13$), indicating that the crossmodal spatial effects obtained in the ‘mirror’ condition do not result from VEP differences in the ‘congruent’ and ‘incongruent’ conditions.

The finding that crossmodal spatial effects are present in the ‘mirror’ condition indicates that when the hands are seen indirectly in a mirror, visual stimuli presented near the hands are not treated as originating in far space in accordance to their physical properties (i.e. in a bottom-up manner), but as peripersonal stimuli, on the base of previous knowledge of mirror-reflecting surfaces (i.e. top-down processing). Indeed, if the true spatial source of visual stimuli was not computed by the brain, and these were coded as far stimuli as suggested by their retinal projections, then we would expect no modulation of ERPs by spatial congruence between tactile and visual stimuli when the latter are viewed in the mirror. That is, no differences should be present between ERPs in response to tactile stimuli when these are coupled with visual stimuli presented in the congruent and incongruent hemispace, as it is the case when visual stimuli are actually presented in far space (see also [23]). Through extensive experience with reflective surfaces in everyday life, humans have learned to recognize their own body parts in mirrors, and to correlate tactile sensations produced by an object (e.g. a comb through the hair) with the distant visual image of the object seen in a mirror (but also see [2] and [15] for accounts of some incorrect judgments and beliefs that people hold about reflective surfaces). Previous behavioural as well as neuropsychological studies also suggest that mirror-reflected visual stimuli may be remapped in terms of their actual spatial location near the body ([19, 21]). The present study provides the first neural evidence in humans that crossmodal spatial effects can occur when visual stimuli are observed as mirror-reflections.

The findings from this study are also in agreement with a neurophysiological study in macaque monkeys in which single-cell activity in response to visuo-tactile stimulation was recorded from the intraparietal sulcus (IPS) contralateral to the monkeys’ stimulated hands ([12]). In this study, a proportion of the bimodal visuo-tactile neurons that responded to a visual probe in proximity to the somatosensory receptive fields (RFs) under direct vision of the hands were also found to respond when the probe was positioned around the hand but the monkeys could only see their hands in a video monitor. Iriki and colleagues [12] suggest that the representation of peripersonal space would incorporate the region of space around the image of the hand in the screen. However, in their study the remapping of visual RFs only occurred after extensive training, during which the monkeys learned to recognize the image of their own hands in the monitor through active movements that required relying on visual information. Although in the present study crossmodal spatial effects between tactile and mirror-reflected visual stimuli do not seem to require any training, it may be noted that these crossmodal effects were only found under conditions in which attention was directed to the stimulated hand[2], and additionally these effects were present at later intervals than under conditions in which visual stimuli were presented and directly viewed in peripersonal space ([23]). Together, this may suggest that the spatial remapping of mirror-reflected visual stimuli according to their true external location does not occur in a completely automatic fashion, and may require additional time.

In addition to the spatial congruence, a main effect of attention was also obtained in the time range of the N140 and N200 components, followed by a sustained negativity (236-300 ms after stimuli onset), reflecting enhanced amplitudes for stimuli presented at (tactually) attended compared to unattended locations, in line with previous reports (e.g. [6, 8]). Importantly, the interaction between the factors attention and condition was not significant, suggesting that the distribution of spatial attention was comparable in the ‘mirror’ and ‘far’ conditions.

Furthermore, a main effect of condition was found in the in the time interval of the N200 and at later latencies (236-300 ms), indicating that in these time intervals ERPs were overall enhanced in the ‘mirror’ compared to the ‘far’ condition. This result may suggest that seeing the visual stimuli near the mirror-reflected image of the hands may enhance ERP amplitudes compared to viewing these stimuli at a distance from the body, regardless of spatial congruence between visual and tactile inputs.

Conclusions

The findings from the present study suggest that crossmodal spatial effects may also be observed for visual stimuli that according to their retinal projections appear as distant ones, once far (mirror) space is remapped as near. Importantly, because here the ‘mirror’ and ‘far’ conditions were comparable with respect to the low-level properties of visual stimuli, as well as to the distribution of spatial attention, the differences between ERPs obtained under these

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[2] Previous studies have shown that crossmodal effects can either occur pre-attentively or be affected by the focus of spatial attention. In particular, crossmodal interactions may be modulated by attention in more complex stimulus conditions (see [24] for a review).

conditions should be ascribed to a higher-level ‘interpretation’ of the actual location of visual stimuli with respect to tactile stimuli in the ‘mirror’ condition.

Acknowledgments: This research was funded by City University London.

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Figure legend

Figure 1 ***(a, b)*** Grand-averaged ERP waveforms elicited in the ‘mirror’ condition ***(a)*** and in the ‘far’ condition ***(b)*** in the 350-ms interval following stimuli onset by tactile non-target stimuli coupled with spatially ‘congruent’ (*solid lines*) and ‘incongruent’ (*dashed lines)* visual stimuli, for attended (*black*) and unattended (*grey*) trials. ERPs are shown for electrodes contralateral to the site of tactile stimulation. In ***(c)*** grand-averaged ERPs are shown together for the ‘mirror’ (*black*) and the ‘far’ (*grey*) conditions, collapsed across attended and unattended trials, at one of the electrode sites included in the analysis (i.e. C3/4; over somatosensory cortex).

Figure

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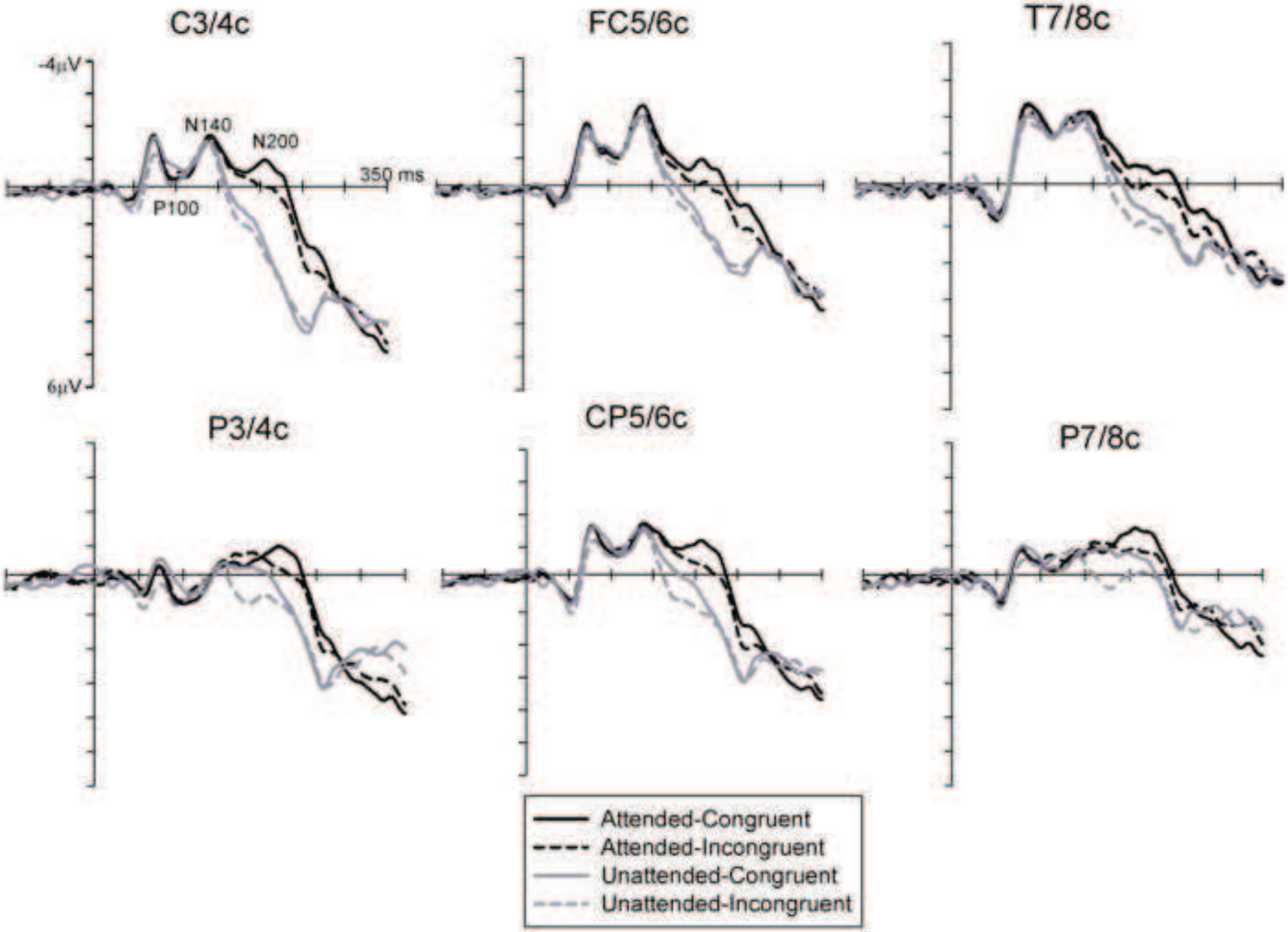

Figure

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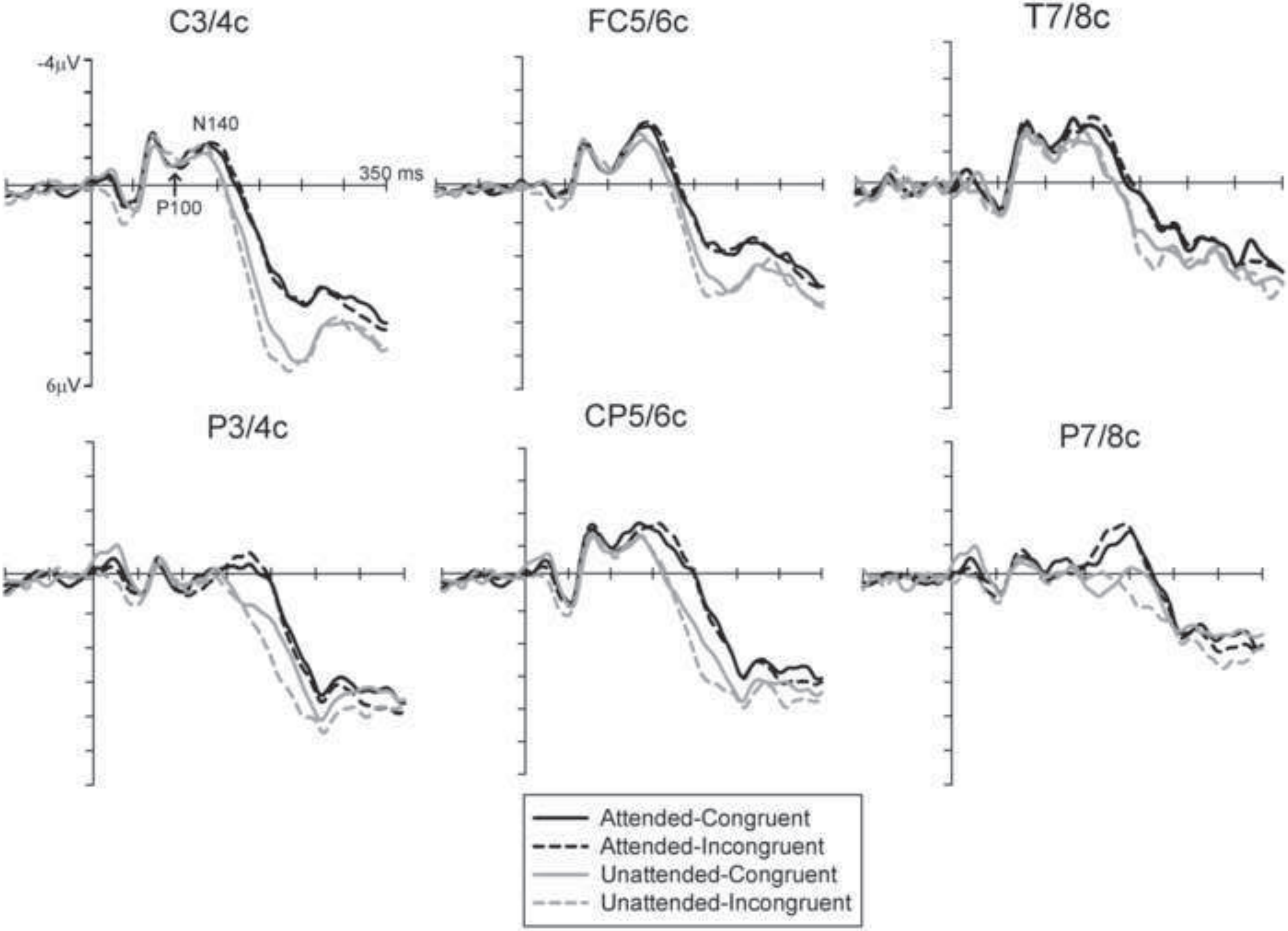

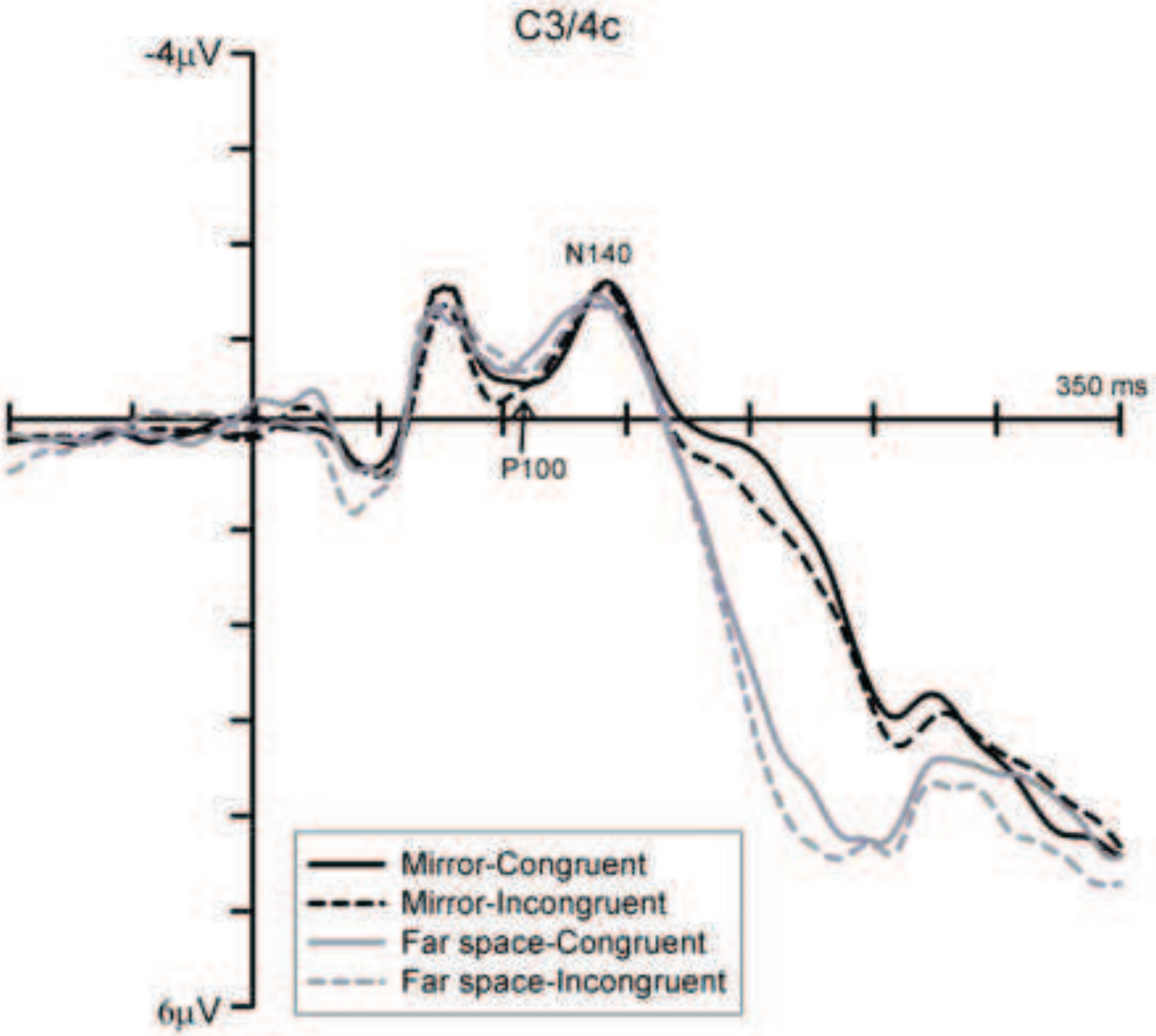
C3/4c
-4µV
6µV
350 ms
N140
P100
Mirror-Congruent
Mirror-Incongruent
Far space-Congruent
Far space-Incongruent