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Electrophysiological Correlates of Motion Extrapolation: An Investigation on the CNV

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Abstract

Motion extrapolation (ME), the ability to estimate the current position of moving objects hidden by an occluder, is critical to interact with a dynamic environment. In a typical paradigm, participants estimate time to contact (TTC) by pressing a button when they estimate the occluded moving target reaches a certain cue. Research using this paradigm has shown that motion adaptation of the occluded area produces a shift in the TTC estimate (Gilden et al., 1995). We examined the effect of motion adaptation on the contingent negative variation (CNV), a frontal electrophysiological

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component (Tecce, 1972) that could reflect the activity of an accumulator (Buhusi & Meck, 2005) for time processing. We predicted that longer TTC estimates due to previous visual motion adaptation would result in a larger CNV because the accumulator can collect more time units. Results showed that motion adaptation actually modulates the CNV, but the CNV amplitude did not correlate with TTC duration, falsifying the accumulator hypothesis. We suggest that motion adaptation interferes with the remembered speed (stored during the visible part of the trajectory) that may be used as input by higher cognitive function to guide the temporal update of target position, regardless of the TTC estimate.

1. Introduction

Predicting the current position of moving objects that are hidden by an occluder for a brief period is of paramount importance to our ability to interact within a dynamic environment. This phenomenon is known as motion extrapolation. Numerous studies have investigated amodal completion during motion extrapolation, showing that during the hidden phase of the moving object the representation of motion is still perceived as continuous despite the absence of physical stimulation (Burke 1952, Michotte 1946; Michotte et al., 1964; 1991), and suggesting that a high-order mechanism computes velocity in the hidden trajectory. Burke claimed (1952) that amodal perception (perception of a complete physical structure when only a part of it affect the sensory receptors) may be used to connect the pre- and post-occlusion modal phases and becomes integral part of the "total sensory experience". Recently the focus has been on the sensory and cognitive processes involved in motion extrapolation (Tresilian 1995; 1999; DeLucia & Liddel, 1998; Makin & Poliakoff, 2011; Makin & Chauhan, 2014; Battaglini, Campana, Casco 2013; Battaglini, Campana, Camilleri, Casco, 2015).

One way to study motion extrapolation is using the time to contact (TTC) paradigm (also known as prediction motion task) in which an object moves toward a visible cue and disappears. In this task, observers have to respond at the time they think the object would contact the visible cue. Recent and consistent evidence indicates that people track the object during motion extrapolation overtly with eye movements, or covertly with the shift of visuospatial attention. It has also been suggested that overt and covert tracking involve similar operations (Makin & Poliakoff, 2011) and similar brain areas (Rizzolatti, Riggio & Sheliga, 1994). However, motion extrapolation may also involve clocking: observers estimate the TTC before occlusion and then use a clocking process to count down time (DeLucia & Liddel 1998; Tresilian, 1995). One hypothesis on how people judge the passage of time comes from the literature on time perception: There may be a dedicated and specialized neural system in frontal cortex (for a review see Ivry & Schlerf, 2008), such as an accumulator (Coull, Cheng & Meck, 2011), that counts pulses generated by an internal pacemaker. In a TTC task, observers can press the response button as soon as the accumulator has collected the number of ticks estimated for the object to reach the visible cue.

Tracking and clocking may not be entirely independent, as a dedicated system for time processing such as an accumulator may work even during tracking. For example, observers can couple the pulses coming from the internal pacemaker with the shift of the visuospatial attention in order to update the object position at the right speed and then press the response button once the accumulator has collected the proper number of pulses. Makin & Chauhan (2014) proposed that a common rate controller, which is like a pacemaker that is functionally coupled to sensory maps, guides extrapolation in different tasks. Indeed, in their experiments they showed similar performance in a classical TTC task and in a number extrapolation task (participants saw a countdown, then the numbers on the screen disappear and they had to press a button when they estimated the number would reach zero). They compared the slope of the time estimation and the variable error (standard deviation of the time estimation) versus the occlusion duration and they found very close values in the two tasks. Moreover, they found that participants who responded earlier (or late) in one task responded earlier (or late) also in the other task. They extended these findings comparing motion extrapolation and extrapolation through color space (pressing a button when a colored disk that will disappear should become the same color of the background) and they found even some evidence for similarities between color and number extrapolation. Even though the presence of an accumulator is not theoretically needed, the common rate controller that guides the internal update of the extrapolation through physical and feature space may be considered similar to a dedicated system that computes the pulses (time units) from a pacemaker.

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The main aim of this study was to use event-related potentials (ERPs) to test the idea of an accumulator as a dedicated system for time processing during motion extrapolation. Only two studies so far have investigated the electrophysiological correlates of motion extrapolation but they focused on perceptual ERP components with a posterior scalp distribution (e.g., occlusion related deflection, ORD) showing that the tracking of visible (actual perception of motion) and occluded targets (motion extrapolation) rely on similar neural systems (Makin, Poliakoff & El-Deredy, 2009; Makin, Poliakoff, Ackerley & El-Deredy, 2012). Instead, we focused on a late ERP component known as the Contingent Negative Variation (CNV), maximal at frontal sites, which is usually elicited by paradigms that involve temporal interval estimation (Tecce, 1972). The CNV is typically found using a chronometric paradigm in which there is an interval between the presentation of two stimuli, a warning stimulus followed by an imperative stimulus, which directs the observer to make a behavioral response. The CNV gradually builds up during the temporal interval between the warning and the imperative stimuli. In the TTC task the stimulus warning is the disappearance of the moving target behind the occluder, whereas the imperative stimulus is an endogenous stimulus corresponding to the estimated time to contact and the corresponding response to indicate so. The CNV is present regardless of the sensory-modality of the stimuli and it is often considered the result of an accumulator of time units (Macar, Vidal & Casini, 1999; Coull et al., 2011). In other words, the CNV seems to reflect temporal accumulation and this may be a fundamental computation involving higher cognitive functions dissociated from immediate sensory input (Meck, Penney & Pouthas, 2008). Indeed some of the main neural generators of the CNV are thought to be in the frontal cortex, including the supplementary motor area and adjacent cingulate cortex (Meck et al., 2008). From this point of view, the CNV may reflect the activity of a supramodal dedicated system for processing time. However, recent empirical findings may not fit well with the notion that the CNV reflects supramodal timing accumulation (Konowicz & Van Rijn 2011, 2014, 2015; Van Rijn, Konowicz, Meck, Ng & Penney 2011; Konowicz & Penney, 2016). Indeed, it has been suggested that the CNV may reflect the activity of a decision-making system (Boehm, van Maanen, Forstmann & Van Rijn, 2014; Van Wassenhove and Lecoutre, 2015) and processes of expectation and response preparation (Konowitz & Van Rijn 2011; Van Rijn et al., 2011) that may be tied to modality-specific processes. Even though the role of the CNV as an index of a pure accumulator is uncertain, the CNV is clearly related to temporal preparation of a response and so it is important to investigate it during a TTC task. Therefore, in this work we asked whether the response time would affect the amplitude of the CNV measured during the occluded phase of motion extrapolation.

A way to modulate the temporal preparation of the response time in a TTC task is to use motion adaptation in the retinal region in which the moving object will be occluded and inducing a motion

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after effect (MAE). MAE is produced by viewing constant motion in one direction (adaptation), which causes a subsequently presented static object to appear to move in the opposite direction (Nishida and Sato, 1995). MAE can also elicit a dynamic effect, where a target moving in the same direction as the MAE-inducing stimulus will subsequently appear to move in the opposite direction, or appear to move slower than it actually is (Mather, Pavan, Campana & Casco, 2008). It has already demonstrated that MAE affects motion extrapolation (Gilden, Blake & Hurst, 1995; Battaglini et al., 2014). Gilden and colleagues (1995) were the first to show that MAE can modulate motion extrapolation by shifting response times in a TTC task depending on the relative motion direction (same vs. opposite) of the adaptor and the moving target. MAE experience, that is in the opposite direction of the motion adaptation, works as a conveyor belt: the "imagery target" (i.e., the speed of the target inferred behind the occluder) is dragged along to the visible cue when MAE experience and target have the same direction (shorter TTC) and pulled back when they have opposite direction (longer TTC).

To summarize, in this work we asked whether the CNV is associated with the response time, that is, whether a more negative CNV is associated with a longer TTC and vice versa. The paradigm used in the present study to investigate motion extrapolation was a classical TTC task (Time to contact task, Benguigui and Bennett, 2010; Benguigui et al., 2004; Huber & Krist, 2004; DeLucia & Liddell, 1998; Makin, Poliakoff, Chen & Stewart, 2008; Peterken, Brown & Bowman, 1991; Rosenbaum, 1975). In addition, in each trial, before the TTC task, participants were adapted in the retinal area where the occluder would be presented, with either leftward or rightward moving textures, which elicited classic MAE. Simultaneously with the TTC task, we recorded and investigate ERPs during the occluded phase.

2. Method

2.1 Participants

Eighteen participants took part in the experiment; ranging in age from 18 to 27; 9 male and 9 female; 1 left handed and 17 right handed. All participants reported normal or corrected-to-normal visual abilities. If their vision was corrected, they were required to wear glasses not contact lenses to minimize blinks. They volunteered as part of the course requirement in return for course credits via an online participation pool or for payment. The electrophysiological data of two participants were excluded from the analysis due to excessive muscle tension and eye movement artifacts. All procedures were approved by the University of Plymouth Ethics Board. Participants were required

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to give informed consent before the study, and they were debriefed fully upon completion of the study.

2.2 Apparatus and Stimuli

The screen monitor was a ViewSonic FuHzion 22" VX2268wm model with widescreen LCD. The refresh rate was set to 100 Hz frame rate with a display resolution of 1680 x 1050 pixels. The contrast was set to default, the luminance was set to maximum, and brightness was set to 300 nit. Participants sat 1.5 meters away from the screen and responded using an RB Cedrus Response Pad. The study was run with MatLab Psychtoolbox (Brainard 1997, Pelli 1997).

2.2.1 Target stimulus (TTC Task)

The target stimulus for the TTC task consisted of a white disk, 0.5 degrees of visual angle in diameter (Fig. 1). The motion trajectory was generated by presenting the target in a new position in successive frames. The visible trajectory started 6.5 deg (left or right side) from the center of the screen, with the target moving at a speed of 3 deg/s. After 3 degrees, the target became occluded (gradually) by an invisible dark rectangle, or occluder (8 x 3 deg, w x h), indistinguishable in colour and luminance from the background (Michelson contrast of the target: 0.99). The end of the occluder was marked by a grey bar (4.5 deg from the center of the screen) at the opposite side of the screen from target initiation (0.3 x 2.5 deg, w x h). This gray bar appeared after the adaptation period. Therefore, the center of the occluder was 0.5 deg right to the center of the screen with target moving rightwards and 0.5 deg left with target moving leftwards. Since the target kept moving behind the invisible occluder at 3 deg/s, the correct TTC was 2.666s.

2.2.2 Adaptation stimuli

Dynamic texture adaptations were composed of a continuous stream of pixels, moving either left or right (Stream condition). In the control condition, a texture created from a static snapshot of the continuous stream was used (Static condition). The speed of the stream was 8 deg/s. The texture (mean luminance of 90 cd/m²) was 7 deg long and 6 deg tall, therefore smaller than the invisible occluder, and was placed at the center of the screen in front of the invisible occluder. The texture was made of 350 x 350 pixels and ended 1 deg before the end of the invisible occluder in order to avoid a MAE effect on the grey bar. Note that only the region in which the target became occluded was adapted.

2.2.3 Fixation Dot

Participants were required to keep their eyes (binocularly) on a fixation dot at all times throughout the experiment. This was to minimize eye movements, produce a stronger MAE, and ensure that participants were not utilizing overt tracking mechanisms. A grey ring 0.4 deg in diameter was presented around the fixation dot in order to avoid MAE on it. The fixation dot was 0.1 deg in diameter (luminance of 100 cd/m²). The spatial position of the fixation dot was 3 deg below the center of the screen. The fixation dot was green during the adaptation and until 1.5s (+ / - 300ms) before the start of the TTC trials, when it turned red to remind participants not to blink or move their eyes during the TTC phase. The fixation dot turned green again once participants had made their TTC response.

2.3 Design

For each participant the moving stream was always unidirectional (always rightwards or always leftwards). Nine participants were randomly assigned to left adaptation and the other nine to right adaptation. In the control condition, they all were adapted with a static texture. The experiment was a repeated measures 2 x 2 design. The first factor was the adaptation conditions (static vs stream). The second factor was the congruency, i.e., direction of the moving target: congruent vs incongruent with the adaptation direction. Although the texture in the control condition was always static, for simplicity trials were labeled as congruent or incongruent according to the experimental block. For example if a participant was adapted with the leftward-moving stream in the experimental block, trials were labeled as congruent also in the control block (static adaptation) when the starting position of the target was in the right part of the screen and the direction was leftward. In both conditions, participants provided a direct estimate of TTC by pressing a button and their response times (RTs) were recorded.

2.4 Electroencephalogram Recording

The electroencephalogram (EEG) was recorded using a BioSemi Active Two system. The experiment was conducted in a dark and noise attenuating chamber. ActiView acquisition software was used to acquire and save the EEG. EEG signals were acquired from participants with an electrode cap, 10/20 system using 64, second generation active Ag/AgCl electrodes. Electrodes were applied with electro-conductive gel to increase conductivity between electrodes and the scalp. Five loose lead flat electrodes were placed on left and right mastoid bones for off-line rereferencing, and under the right eye and on the two on outer canthi to monitor ocular artifacts.

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Signals were amplified with a low pass of 4 KHz and direct current (DC) mode. Signals were sampled at 4096 Hz and downsampled off-line to 512 Hz.

2.5 Procedure

Participants were seated in a separate room and placed 150 cm away from the screen. They were instructed to remain as still as possible, and to keep their eyes on the fixation dot at all times. Participants were informed that they should not blink when the fixation dot was red. The experiment was divided into 6 intermixed blocks, 3 per adaptation condition (moving vs. static). Since each block consisted of 40 trials, there were 120 trials per adaptation condition, for a total of 240 trials. After each block there was a short break, which lasted until the participants were ready to carry on with the task. Regardless of adaptation type in each block, the adaptation was 60s for the first trial and 10s for subsequent trials (top-up adaptation, Gilden et al., 1995). For each participant, the adaptation was always in the same direction and the congruency (congruent vs. incongruent) depended on the direction of the moving target, from left to right on half the trials, and from right to left on the other half. Each TTC trial was initiated by a target appearing 10 ms after the end of the adaptation phase, either on the left or right side of the screen with equal probability and travelling horizontally across the screen. Participants were instructed to press an assigned response button when they estimated the moving target would reach the grey bar at the opposite side of screen (Fig. 1). The TTC estimates were calculated as the time of visible (1 second) + invisible trajectory until button press.

3 RESULTS SECTION

3.1 Behavioural Results

To follow the results, it may be useful to be reminded of the conveyor belt metaphor to conceptualize the MAE experience. In this metaphor, the "imagery target" is pulled along to the visible end of the occluder when MAE experience and target have the same direction (shorter TTC) and pulled back when they have opposite direction (longer TTC). To confirm the result a mixed ANOVA on the TTC data was conducted with congruency (congruent vs. incongruent) and adaptation condition (stream vs. static) as a within-subjects factors, and adaptation direction (left

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vs. right) as between-subjects factor. Bear in mind that trials in the static condition were labeled as congruent or incongruent according to the corresponding experimental block. For example, when leftward adaptation was used in the experimental block, trials in the corresponding control block (static adaptation) were labeled as congruent when the starting position of the target was in the right part of the screen and it moved leftwards.

Texture Adaptation

ANOVA revealed a significant main effect of adaptation condition ($F_{(1,17)} = 11.71$, $p = 0.003$, $\eta^2_p = 0.42$) showing that the TTC was shorter after the adaptation with a stream than static stimulus, and congruency ($F_{(1, 17)} = 7.53$, $p = 0.014$, $\eta^2_p = 0.32$) indicating that the TTC was longer on congruent than incongruent trials. The interaction between adaptation condition and congruency was also significant ($F_{(1, 17)} = 6.07$, $p = 0.025$, $\eta^2_p = 0.26$). Planned pairwise comparisons were computed using Bonferroni correction. This further analysis revealed that the TTC after static adaptation was longer than after stream adaptation for both congruent ($p < 0.035$) and incongruent ($p < 0.001$) trials (Fig. 2). Moreover, in the adapting stream condition the TTC was significantly longer in the congruent than incongruent trials ($p < 0.01$). This is consistent with our predictions and with a previous work (Gilden et al., 1995). However, contrary to expectations, the TTC in the static adaptation condition was significantly longer than the TTC in the congruent trials in the stream adaptation condition.

3.2 ERP analyses

Raw EEG data was low-pass filtered off-line at 30 Hz prior to analyses. EEG recordings were inspected for artifacts manually using the EEGLab plugin ERPLAB (Lopez-Calderon & Luck, 2014). An average of 4 trials (SD = 4) were rejected per participant. Data were rereferenced off-line to the average of the two mastoids.

3.2.1 CNV

Mixed ANOVAs were conducted on the mean amplitude of the average ERPs for each participant. The within-subject factors were adaptation condition (stream vs. static), congruency (congruent vs. incongruent), and electrode site. Electrode sites were chosen based on the existing literature (Macar & Vidal, 2003; Macar et al., 1999; Mento, Tarantino, Sarlo & Bisiacchi, 2013; Kononowicz & Van Rijn 2011, Liu et al., 2013), and included five midline locations, Fpz, AFz, Fz, FCz and Cz, and two lateral frontal pairs; F1-F2 and, FC1-FC2. The between-subject factor was

the direction of the adaptation texture (left vs. right). The time window of interest was from the time when the target became occluded to 1500 ms. A longer epoch would have resulted in a substantially higher number of eye movement artifacts, since participants were free to blink after providing their response.

3.3 Electrophysiological Results

CNV

There was a robust CNV following target occlusion (Fig. 3). The between-subject factor of adaptation direction (left vs. right) was not significant, and so the data from the two directions were collapsed. The CNV was significantly more negative in the stream than static condition ($F_{(1, 14)} = 6.66$; $p = 0.022$, $\eta^2_p = 0.32$). The main effect of site was also marginally significant ($F_{(3.595, 50.336)} = 2.68$; $p = 0.048$, $\eta^2_p = 0.16$). The CNV was largest at site F1, but pairwise comparisons with Bonferroni correction did not show significant differences between any sites. Importantly, the interaction between adaptation condition and congruency was also significant ($F_{(1,15)}=8.72$ $p=0.011$, $\eta p^2 = 0.38$). Pairwise comparisons with Bonferroni correction showed that in the congruent trials the CNV was more negative in the stream than in the static condition ($p<0.01$). Moreover in the stream condition, the CNV was more negative in the congruent than incongruent trials ($p<0.04$). None of the other interactions were significant. In sum, these results showed that the CNV is more negative after adaptation to a stream moving in the same direction as the target than in the opposite direction or after static adaptation (Fig. 3). A further analysis was carried out in order to assess whether there was also a CNV before occlusion, since this interval is likely to be timed as well. Thus, we conducted a repeated measures ANOVA on the mean amplitude of the average ERPs for each participant with time window (mean amplitude between -200 and -101 ms vs between -100 and 0 ms), adaptation condition (stream vs. static), congruency (congruent vs. incongruent), and site (Fpz, AFz, Fz, FCz, F1, F2, FC1, FC2) as factors. Results revealed only a significant effect of time window ($F_{(1,15)}=16.34$ $p=0.001$, $\eta p^2 = 0.52$); the mean values indicated that the time window between -100 and 0 ms was more negative (-0.229 vs 0.234 mV). This result supports the hypothesis that there is a CNV also during pre-occluded motion, but that the CNV is not affected by the adaptation and congruency manipulations.

3.4 Correlation at individual trials level between CNV amplitude and estimated TTC

In order to test explicitly whether there is a relationship between CNV amplitude and estimated TTC we measured these two variables on each trial for each participant (in the four condition by

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congruency combinations separately), and examined the correlation between the two. In the static incongruent condition only one out of sixteen participants showed a significant correlation between the TTC estimated and the CNV amplitude (slope = -5.7; $R^2 = 0.1$, $p = 0.014$), whereas none showed significant correlations in the static congruent condition. In the stream incongruent condition two out of sixteen participants showed a significant correlation (Participant 1: slope = -5.8; $R^2 = 0.11$, $p = 0.01$; Participant 2: slope: -4.9; $R^2 = 0.1$, $p = 0.017$) whereas in the stream congruent condition only the correlation of one participants was significant (slope: -9.8; $R^2 = 0.1$, $p = 0.016$). Only 4 out of 64 correlations are significant and the R^2 was never higher than 0.12 indicating a weak correlation. Therefore we conclude that our data do not support the hypothesis that longer TTC estimates lead to larger CNVs.

4. Discussion

The main findings from this study can be summarized as follows. First, in the stream adaptation condition time to contact is shorter when adaptation is in the opposite than in the same direction of the moving target, showing that stream adaptation modulates motion extrapolation. This makes sense in the context of the conveyor belt metaphor of the MAE experience (opposite direction respect to the motion adaptation). Indeed the "imagery target" (i.e., the speed of the target inferred behind the occluder) is dragged along by the visible end of the occluder, reducing the TTC, when MAE experience and target move in the same direction, and pulled back, lengthening the TTC, when they move in opposite directions. Interestingly, stream adaptation reduces estimates of TTC relative to static adaptation regardless of the congruency between motion adaptation and the moving target. Second, the TTC task elicits a robust CNV, which is modulated by the congruency between motion adaptation and the moving target, but is dissociated from the length of the TTC estimate.

The behavioral results are surprising. Consistent with previous studies, in the stream adaptation condition the time to contact estimation was shorter in incongruent than congruent trials (Gilden et al., 1995, Battaglini et al., 2015). However, contrary to what was expected, the time to contact in the static adaptation condition was significantly longer than the time to contact in the congruent trials in the stream condition. A possible way to explain this results is to assume that dynamic adapting stimulus can change temporal perception (Kanai et al., 2006; Burr et al., 2007; Johnston et al., 2006), speeding-up the passage of time. Indeed, it has been shown that stimuli in motion are

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perceived to last longer (Kaneko & Murakami, 2009); therefore, it is possible to speculate that the moving adaptor accelerates the collecting rate of an internal pacemaker, which therefore accumulates time units faster and leads to shorter TTCs.

Our electrophysiological data revealed a CNV during the visible motion period, but it was not modulated by adaptation condition or congruency. More interesting, our data showed a robust CNV during motion extrapolation. Furthermore, longer TTC estimation due to motion adaptation was associated with a larger CNV. At first sight, the larger CNV after motion adaptation is in line with the hypothesis that this negative component reflects the activity of an accumulator that can collect more time units (Buhusi & Meck, 2005) because of longer time to contact estimations and is in line with the existence of a dedicated system for time processing. Indeed, during the stream adaptation condition longer interval estimation was associated with a greater CNV amplitude in Macar et al.,'s (1999) work. However, in our static adaptation condition the time to contact estimation is even longer, but the CNV is not larger than in the stream adaptation condition; rather, it is significantly smaller. One could argue that if the moving adaptor is perceived to last longer and it actually increases the collecting rate of the internal pacemaker, then the CNV might be more negative even with shorter TTC because more time units will be collected. To address this possibility, we tested the relationship between CNV amplitude and estimated TTC separately for all four condition by congruency combinations. This way, the collecting rate of the internal pacemaker should be constant in each condition and it was possible to test whether there was a correlation between the estimated TTC and the amplitude of the CNV. However, we found no sign of a linear relationship in any condition, falsifying the hypothesis that longer estimated TTC is associated with a more negative CNV amplitude. This is in line with recent studies (Kononowicz & Van Rijn 2011; Van Rijn et al., 2011) that using a strong methodology and high statistical power failed to show a correlation between the reproduction of a time interval and CNV amplitude.

These results indicate that CNV amplitude during motion extrapolation does not behave as a simple accumulator would. An alternative explanation is that the CNV reflects the activity of a prediction and decision-making system. In particular, Boehm and colleagues (2014) suggested that the CNV reflects the cognitive preparedness to process information and its amplitude depends on how much sensory information is gathered before engaging in a decision. MAE interference in the stream congruent condition may alter the expectancy of reappearance and motor preparedness, increasing the sensory information gathered in the decision-making system and resulting in a larger CNV.

Given that our data does not seem to support the idea of the CNV as an index of the workings of an internal pacemaker and accumulator, an important question is whether one can still consider the

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CNV as a temporal and expectancy index. The following arguments suggest that this may be the case. First, we did not falsify the existence of a dedicated system but only the correlation between the length of TTC estimate and CNV amplitude. Indeed a dedicated system can work in a different way from a simple accumulator or could not result in a CNV (Van Rijn, Gu & Meck, 2014). Instead, this work showed that MAE affects not only the response time in a TTC task but also the amplitude of the CNV. In neural terms, this may indicate that prior and prolonged activation of motion sensitive areas (motion adaptation) affects the subsequent activity in the frontal areas that generate the CNV. We propose the following interpretation: the remembered speed of the target relies on V5, a visual areas specialized for motion perception. Indeed McKeefry, Burton & Vakrou (2007) reported a consistent link between area V5 and visual short-term memory, and Campana, Cowey and Walsh, (2006) showed that this area is fundamental for priming for motion direction. Furthermore, this area is implicated in MAE (Tootell, Reppas, Dale, Look, Sereno, Malach & Rosen, 1995; Théoret, Kobayashi, Ganis, Di Capua & Pascual Leone, 2002). MAE modulates activity in V5, which may change not only the way V5 collects and stores information from the visible speed of the target, but also how it uses it to create an internal representation of the moving target during occlusion. This information may be used to guide spatial updating of the target by a mechanism such the common rate controller proposed by Makin & Chauhan (2014), which may be implemented in brain regions (including frontal cortex) that are implicated in CNV generation. When the input coming from motion sensitive visual areas is degraded because of previous motion adaptation in the same direction as the target, frontal areas may need to work harder for spatial updating and that could lead to a more negative CNV, regardless of TTC estimate. In contrast, prior motion adaptation in the direction opposite to that of the target should not interfere with its remembered speed because the memory of speed is selective for motion direction (Bisley & Pasternak, 2000).

Makin and Poliakoff (2011) stressed that the shift of the visuospatial attention to an external location may be the basis of motion extrapolation and that this process alone may be sufficient to explain it. Although visuospatial tracking is fundamental for motion extrapolation (Makin & Poliakoff, 2011; Makin et al., 2012), our study showed an electrophysiological correlate over frontal areas typically associated with timing, expectancy or decision-making. Moreover, we showed how this frontal activity could be modulated by previous exposure to real motion. A sensorial-cognitive model that aim to explain motion extrapolation completely should consider also these aspects.

To summarize, the computation of motion extrapolation probably relies on several neurocognitive mechanisms. In this study, the focus was on the visual and timing mechanisms and on the possible

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correlates of motion extrapolation in a TTC task. Results showed that motion adaptation modulates TTC estimates as well as the amplitude of the CNV, however not in accordance with the accumulator (pacemaker) hypothesis. These results suggest that there is a complex neural network for computing motion extrapolation with key nodes in regions involved in cognitive control processing. However, it is likely that this study has investigated only a small part of the neural network that computes motion extrapolation. In fact primate neurophysiological data and fMRI studies (Barborica and Ferrera, 2003; Shuwairi, Curtis & Johnson 2007; Nagel et al., 2006; Ding, Powell & Jiang, 2009; Kaas, Weilgelt, Roebroeck, Kohler & Muckli, 2010) showed a large neural network active during motion extrapolation including visual (V5) and frontal areas (DLPFC, FEF, SEF) but also the cerebellum, insula, inferior parietal lobe, cuneus, intra parietal sulcus and anterior cingulate cortex. Even V1 seems involved, indeed in a very ecological TTC task with approaching motion it was demonstrate that V1 increase activity with increasing likelihood of reporting a collision, indicating top-down modulation from higher cognitive areas (Coull, Vidal, Goulon, Nazarian & Craig, 2008). Further work will be needed to parse the contribution of these different brain areas to motion extrapolation.

Contribution. Luca Battaglini and Giorgio Ganis contributed to all stages of the study. Bethany Rose Isaacs and David Bridges contributed to data collection and analyses. Clara Casco contributed to the initial idea for the study.

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Figure 1. Diagram of a trial in a TTC task, in the 4 possible conditions. *After the adaptation, the moving target travelled along a horizontal linear path at a constant speed until it slid behind an invisible occluder (white dotted rectangle). Participants were instructed to assume that the target maintained a constant speed and trajectory behind the occluder and to respond when they believed that the leading edge of the target had reached the grey bar, marking the edge of the occluder.*

Figure 2. Estimated Marginal Means: *TTC estimates were longer in the static than in the stream adaptation condition. Moreover, TTC estimates were longer for the congruous than incongruous stimuli in the stream adaptation condition, but not in the static adaptation condition. Correct TTC was 3.66 (1 sec of visible trajectory + 2.66 sec of occlusion).*
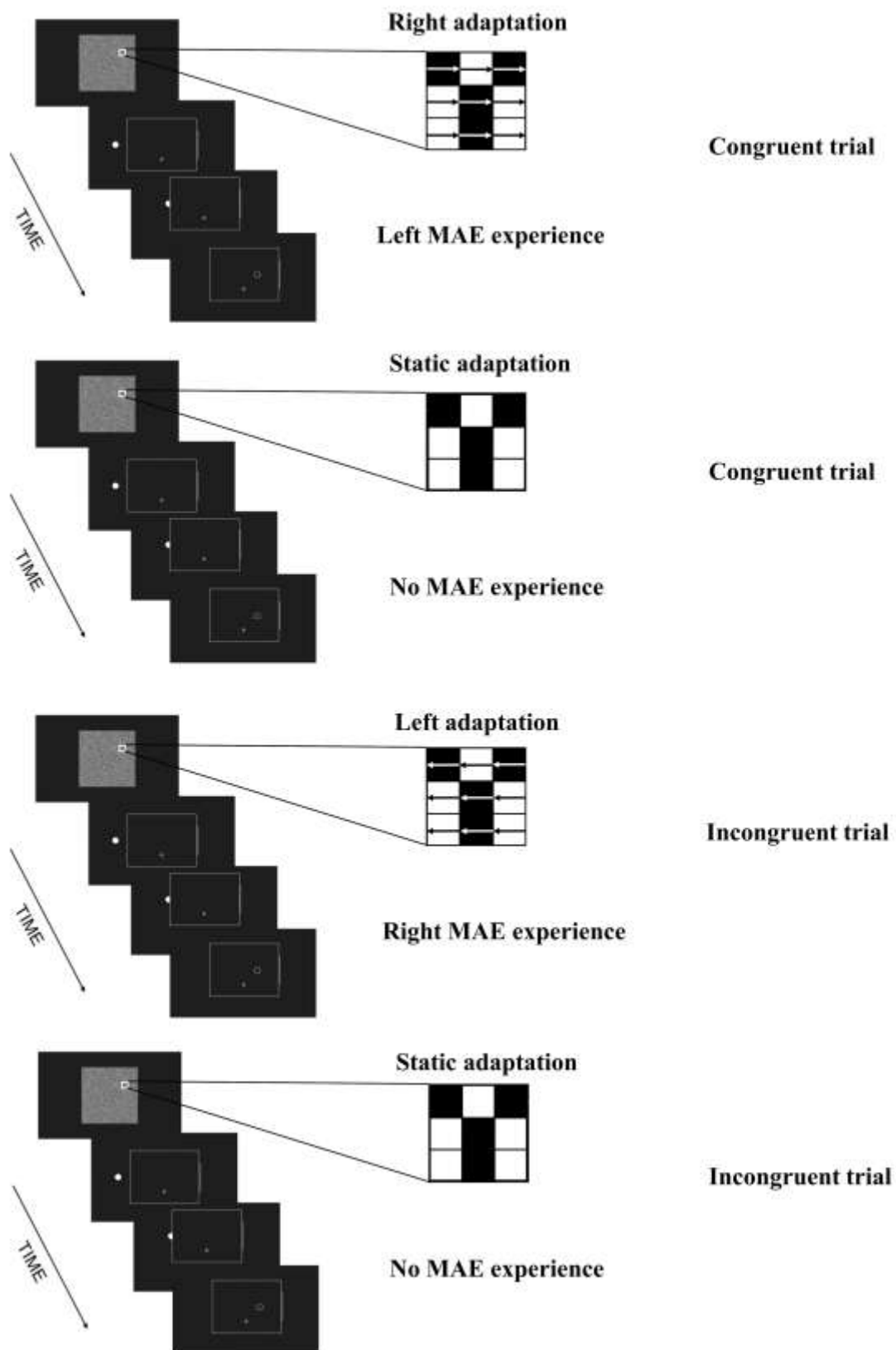
Figure 3. Electrode Sites of Interest: *CNV in the Texture Adaptation Experiment.*
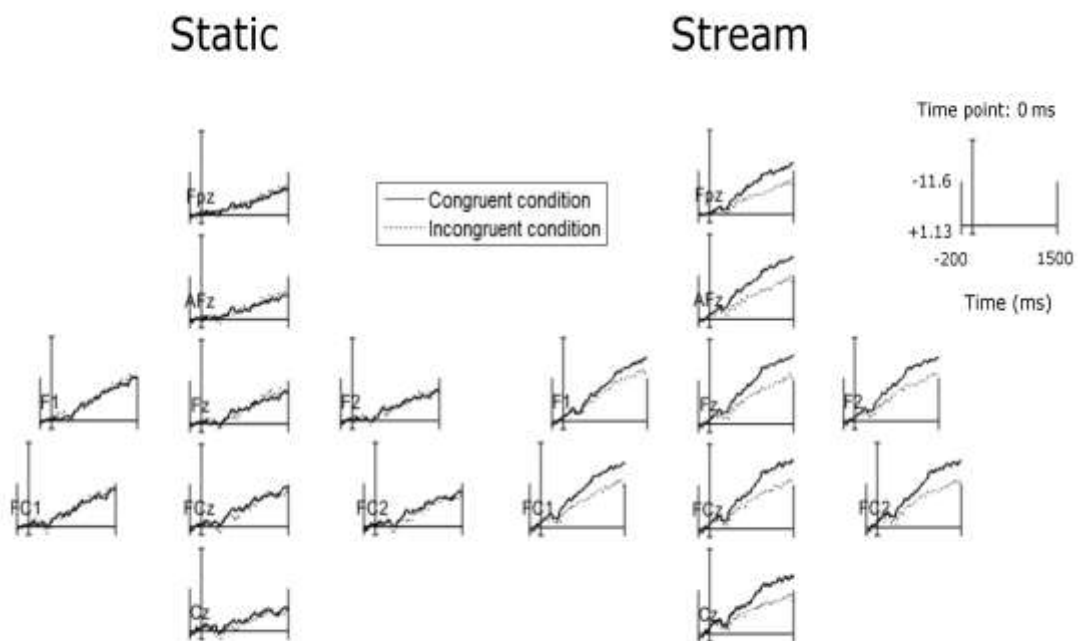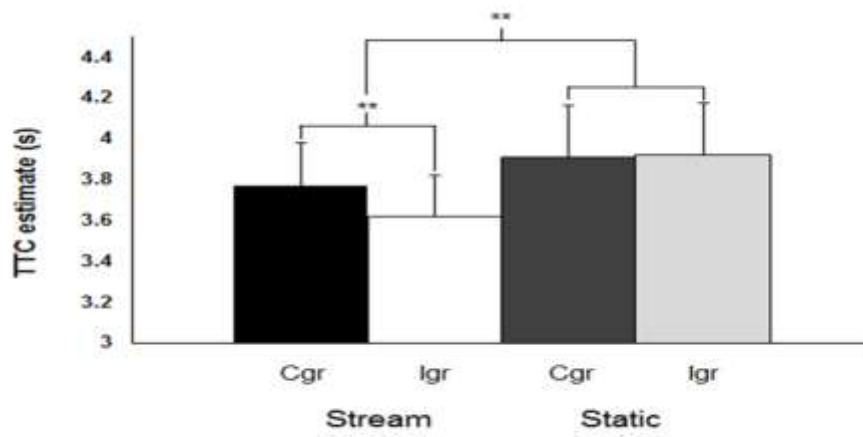
Figure 4. Grand average of the ERP waveform obtained by collapsing across the nine frontal and central electrodes of interest (Fpz, AFz, F1, Fz, F2, FCz, FC1, FC2, Cz) time-locked to the disappearance of the moving target.
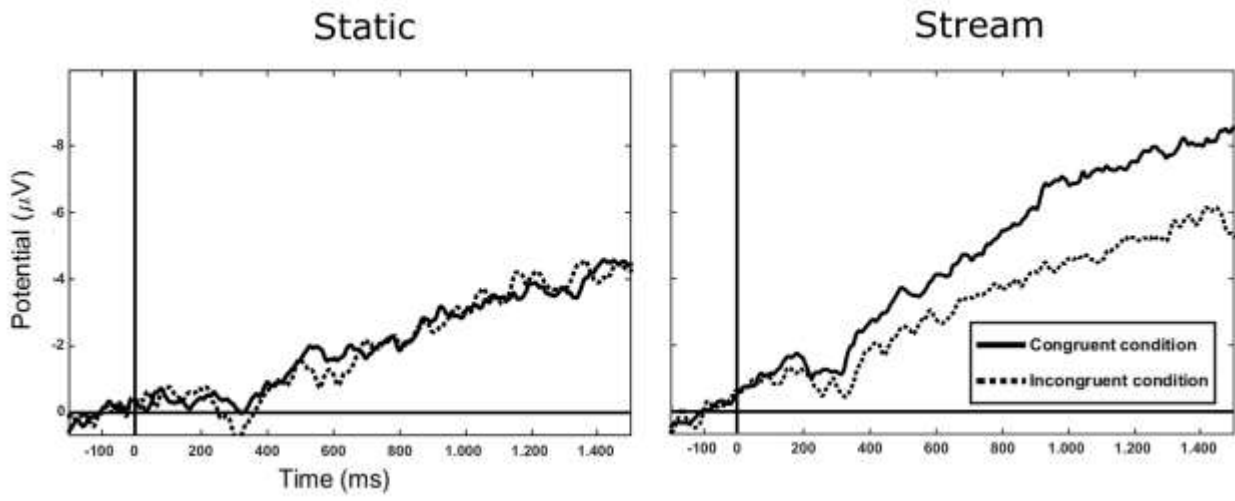
Highlights

- *Time to contact task elicits a Contingent Negative Variation (CNV).*
- *Previous motion adaptation can modulate the amplitude of the CNV.*
- *The amplitude of the CNV does not correlate with the time to contact estimation*
- *Visual and higher cognitive functions interact during motion extrapolation.*

Static

Stream