Sensory and Motor Systems

The Readiness Potential Correlates with Action-Linked Modulation of Visual Accuracy

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Abstract

Visual accuracy is consistently shown to be modulated around the time of the action execution. The neural underpinning of this motor-induced modulation of visual perception is still unclear. Here, we investigate with EEG whether it is related to the readiness potential, an event-related potential (ERP) linked to motor preparation. Across 18 human participants, the magnitude of visual modulation following a voluntary button press was found to correlate with the readiness potential amplitude measured during visual discrimination. Participants’ amplitude of the readiness potential in a purely motor-task was also found to correlate with the extent of the motor-induced modulation of visual perception in the visuomotor task. These results provide strong evidence that perceptual changes close to action execution are associated with motor preparation processes and that this mechanism is independent of task contingencies. Further, our findings suggest that the readiness potential provides a fingerprint of individual visuomotor interaction.

Key words: action and perception; EEG; efference copy; ERP; motor-induced visual modulation; readiness potential

Significance Statement

Vision and motor action need to be closely synchronized. Performing, or even programming, an action changes our visual perception: the ability to discriminate visual stimuli typically decreases transiently at the time of execution of a movement such as a button press. In the present study we demonstrate that the magnitude of this perceptual modulation is predicted by the strength of an EEG premotor signal that precedes the action execution, the readiness potential: the greater the magnitude of this signal, the weaker the visual modulation. We suggest that this mechanism may be exploited by the brain to synchronize and coordinate action and perception over time.

Introduction

To act effectively on the sensory information that we receive every moment of our daily life, action and perception require precise temporal coordination. The neural mechanisms underlying sensorimotor interactions are complex and not fully understood. However, they likely involve a premotor signal (Helmholtz, 1866; Sperry, 1950; von Holst and Mittelstaedt, 1950), that prepares the visual system for the sensory consequences of a self-initiated action. This may account for a range of phenomena, including saccadic suppression, where visual sensitivity is suppressed for a short time around saccadic execution (50 ms before to 50 ms after; Burr et al., 1994). The function of this suppression may be to maintain visual stability during eye movements by suppressing transient and spurious motion signals caused by the rotation of the eyeball. However, similar suppressive effects have been reported for a variety of sensorimotor tasks involving different body
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A total of 18 volunteers (including two authors; mean age ± SD: 27 ± 2, 10 women and 8 men) participated in the study. The sample size was chosen based on previous experiments in the same field of research (Stenner et al., 2014a; Tomassini et al., 2017). The experimental procedures are in line with the Declaration of Helsinki and were approved by the local regional ethics committee. Written informed consent was obtained from all participants. This includes consent to process and preserve the data, and publish them anonymously.

The visual stimuli were generated with Psychtoolbox for MATLAB (MATLAB r2017b, The MathWorks, Inc.) and displayed on a γ-calibrated Display+ monitor (Cambridge Research System, resolution of 1920 × 1080 pixels, refresh rate of 120 Hz). A custom response box was connected with a Ni-DAQ USB-6001 to the experimental computer to record button-press timing and send triggers to the EEG device.

EEG was recorded using a 32 active-channel wireless g.Nautilus system, with a sampling rate of 500 Hz. The scalp electrodes were positioned according to the 10–20 international system and the reference electrode on the right earlobe. The impedance was checked before each recording and kept below 50 kΩ.

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The present study investigates the link between the readiness potential and differences in visual accuracy at around the time of action execution and demonstrates that the amplitude of the readiness potential is associated with the modulation of visual perceptual accuracy of stimuli presented around the onset of the action.

Materials and Methods
Participants

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Apparatus

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Stimulus and procedure

The experiment consisted of two tasks: a visuomotor, and motor-only task, completed in separate blocks over two recording sessions on different days. In session 1,
participants performed the motor-only task (100 trials) and two blocks of the visuomotor task (162 trials per block). In session 2, they performed another two blocks of the visuomotor task (162 trials per block). Before each session, participants completed a training block to familiarize themselves with the tasks. In total, we collected 648 trials per participant for the visuomotor task and 100 for the motor-only task. Two (out of 18) participants who participated in the initial pilot phase of the experiment underwent three additional sessions (six blocks), bringing the total number of visuomotor trials to 1620 each. Given the result congruency between the initial two sessions with the later three sessions, we pooled all trials for these two participants.

**Visuomotor task**

The visual stimulus in the visuomotor condition comprised two vertical gratings ($32^\circ \times 16^\circ$, 50% contrast, random phase) presented for 8.3 ms (one frame) randomly in the right or left visual field. The two gratings were always presented in the same hemifield and placed 3° left/right from a small fixation square displayed at the center of the screen. The gratings had a fixed spatial frequency of 1 and 1.1 c/° (10% difference), randomly presented in the upper or lower part of the monitor (see Fig. 1A). Participants were instructed to maintain their fixation on the small center square and press a key (with the index finger of the right hand) to start each trial. The visual stimulus was presented with 18 possible stimulus delays after the button press, chosen randomly on each trial in the interval between 16 and 816 ms to avoid a stereotypical allocation of subject attention to very late or very early after the action onset. The random stimulus presentation to the left or right visual field and the short stimulus exposure aimed to minimize the number of saccades coinciding with the stimulus which could impair discrimination performance. The delays had a denser sampling in the first 350 ms from button press (33-ms bins) and sparser sampling at later delays (66-ms bins). The task was to indicate which grating (upper or lower) had the higher spatial frequency. Participants were instructed to maintain fixation on the small center square and press a key when a grating started, and to wait at least 1.5 s from the stimulus onset before giving a verbal response, coded by the experimenter. They waited at least another 1.5 s before starting the next trial. Participants were trained to adhere to the trial timing. The mean interval ($\pm 1$ SD) between successive button presses was 5.46 $\pm$ 0.88 s. Participants waited on average 2.6 $\pm$ 1 s from stimulus onset before providing a verbal response. They were warned when their responses occurred too early, but the trials were not excluded from the analysis (<1% of trials had responses below 1 s).

**Motor-only task**

In the motor-only task, participants simply had to press the button and look at the fixation point in the center of the screen. No visual stimulus was presented in this condition and, therefore, no response was required. As in the visuomotor condition, we asked participants to wait at least 1.5 s between successive button presses (mean and SD of interbutton-press interval: 2.75 $\pm$ 1.01 s).
Data analysis

The EEG data were referenced to a common average and high pass filtered with a cutoff of 0.2 Hz (Blackman sinc FIR filter with a transition bandwidth of 0.4 Hz and filter order of 6876) using the MATLAB toolbox EEGLAB in combination with the plugin firfilt. Trials were epoched relative to the button press from −0.5 to 0.2 s. The ERPs were low-pass filtered at 40 Hz with an IIR Butterworth filter from the MATLAB toolbox Fieldtrip. As our primary interest was in the preaction activity, we defined an EEG baseline centered at action-onset (−0.05 to 0.05 s from key-press). In this condition, the readiness potential typically starts from a positive voltage and reaches 0 at the time of button press. Almost identical waveforms and topographies are obtained when using an earlier baseline (−0.5 to −0.4 s; Extended Data Figs. 1-1 and 1-4). As participants were prone to blink at a high frequency during the interval from −1 to −0.5 s from button press (see next paragraph), EEG activity >0.5 s before action onset was not suited for baseline correction.

To identify and exclude trials with blinks, ICA was run on the continuous high-pass filtered data (informed ICA algorithm; Bell and Sejnowski, 1995) with a cutoff of 1 Hz (Blackman sinc FIR filter with a transition bandwidth of 2 Hz). After visually identifying and extracting the component related to blinks following standard criteria (left-right symmetry, frontal topography), we calculated the z score of the blink-related component, for each trial, in the interval −1–0.2 s. As eyelid-induced artifacts typically last for 200 ms (Plochl et al., 2012), trials with peaks of activity above 2 z scores within −0.7 and 0.1 s from button press were excluded from further analysis. The average percentage of trials excluded was 7.6% and 9.5% in the visuomotor and motor-only tasks respectively (see Extended Data Fig. 1-2). To overcome this limitation, we also verified fixation in 5 participants by measuring eye movement with an Eyelink 1000 (SR Research; see Extended Data Fig. 1-3 for results).

Our analyses focused on readiness potential activity. We determined the eight electrodes that recorded the strongest readiness potential activity (i.e., stronger negative deflection) by evaluating the slope of a linear regression of the grand-average ERPs in the interval −0.5 to −0.02 s from button press in the visuomotor condition. Electrodes FC1, C3, CZ, CP5, CP1, CP2, P3, and PZ were selected given the strongest negative slope (mean ± SD: −2.02 ± 0.84 µV/s; see the topographic plot in Fig. 1B). Applying the same procedure, the same electrodes were selected for the motor-only condition (see Extended Data Fig. 1-4). Previous studies confirm that these electrodes are the ones typically expressing the strongest readiness potential response (Neshige et al., 1988; Ikeda et al., 1992; Shibasaki and Hallett, 2006; Di Russo et al., 2017).

To estimate modulation of perception around the time of action execution, trials from the visuomotor task were divided into two datasets: short and long action-stimulus intervals (ASIs). The short ASIs condition included trials in which the visual stimulus appeared no later than 120 ms after the button press; the long ASIs condition included trials with the visual stimulus occurring later than 600 ms after the button press. An exponential fit to the data confirmed a decrease in visual accuracy for ASIs close to the action, with accuracy reaching asymptote around 100–150 ms after the button press ($F_{3,19}=14,138.6; p < 0.001$; Fig. 1C). The modulation of visual accuracy was estimated as the difference between the average accuracy in long versus short ASIs trials. The mean (±1 SD) number of trials across participants was 123 ± 11 and 129 ± 13 for short and long ASIs, respectively; for the two participants with more sessions, the mean number of trials was 318 ± 5 and 351 ± 9 for short and long ASIs, respectively. The analysis of visual response accuracy was repeated using only trials in which the stimulus occurred <100 ms after the button press in the short condition.

To estimate the amplitude of the readiness potential, we computed mean amplitudes over the electrodes of interest for the period −500 to −100 ms relative to button press (see Fig. 1B). These estimations were done separately for the visuomotor task and motor-only task. To test how the amplitude of the readiness potential relates to the magnitude of the modulation in performance, we computed the Pearson’s correlation coefficient across subjects (see also Extended Data Fig. 2-2 for a description of the visual-evoked potential results and methods, in the two conditions).

Results

Eighteen volunteers were asked to indicate which grating (upper or lower) had the higher spatial frequency when two brief stimuli were presented randomly in either the left or the right visual hemifield, with 18 possible delays from action execution (ranging from 16 to 816 ms). Participants performed the task with an overall accuracy of 74 ± 2% (mean and standard error), all within 60–90% of accuracy. For each participant, modulation of visual accuracy was estimated as the difference between the average perceptual accuracy for stimuli presented far away from the action (long ASIs, with visuomotor delays >600 ms) and those presented close to the button press (short ASIs, with visuomotor delays <120 ms). Overall, long ASIs accuracy was higher than the short ASIs one, with an average improvement of ~5% (Fig. 1D). A two-tailed paired-sample t test confirmed that visual accuracy was higher for long than for short ASIs ($t_{17}=3.55, p = 0.002$). To assess whether this perceptual modulation was related to the position of the visual stimulus (left or right visual field), we split the dataset into stimuli presented to the left and stimuli presented to the right hemifield and contrasted the size of the modulation effects. The effect was not significantly different for stimuli presented on the left and right visual field ($t_{17}=1.08, p = 0.282$), suggesting that the modulation effect was independent of the hemifield in which the stimulus occurred.

To be able to test for a correlation between the strength of the readiness potential and the modulation of visual perception, we computed the individual mean amplitudes of the readiness potential over the a-priori defined electrodes of interest: FC1, C3, CZ, CP5, CP1, CP2, P3, and PZ, for the temporal window −500 and −100 ms before the button press (Fig. 1B, light blue curve). We correlated the difference in visual accuracy for long and short ASIs with the amplitude of the readiness potential in the visuomotor
delays larger than 100 ms (Blakemore et al., 1999; Aliu et al., 2009). To make our results more comparable to the existing literature, we replicated the correlation analyses by restricting the short ASI delays below 80 ms. Visual accuracy for these shorter ASIs was lower compared with long ASIs ($r_{(17)} = 3.125; p = 0.006$), and was significantly correlated with the amplitude of the readiness potential for both the visuomotor ($r_{(18)} = -0.556; p = 0.016$) and the motor-only condition ($r_{(18)} = -0.502; p = 0.033$).

Discussion

The characteristics of readiness potential, a slow EEG response that emerges during action preparation, has been associated with many functional differences that affect how action and perception interact over time (Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018; Travers et al., 2021) and perceptual confidence (McAdam and Rubin, 1971). Despite this evidence, it is still unknown whether an association exists between this ERP component, indicative of motor preparation, and the effect of voluntary actions on visual perceptual accuracy. Here, we demonstrate that this motor-induced modulation of visual accuracy is associated with the readiness potential. Specifically, our findings show that the magnitude of this modulation correlates with the readiness potential amplitude in both visuomotor and motor-only tasks. This suggests that the processes underlying the readiness potential are linked to the modulation of visual perception around the time of action execution, and readiness potential may be a fingerprint of individual visuomotor interactions.

We found that discrimination accuracy for visual stimuli triggered by participants’ button press was significantly reduced for stimuli presented within the first 100 ms after the button press, as compared with when the visual stimuli occurred later in time (>600 ms). Given the difficulties of including a passive condition, balanced for sensory expectation and attentional load, we cannot establish whether the modulation is associated with peri-action performance suppression or, rather, post-action performance enhancement. However, previous findings have shown consistently reduced perceptual accuracy for visual stimuli triggered by voluntary hand movements compared with externally triggered stimuli (Cardoso-Leite et al., 2010; Stenner et al., 2014a; Vasser et al., 2019), suggesting a suppression of performance in our experiment as well. Interestingly, the temporal dynamic of the current modulation mimics the known dynamic of sensory attenuation in the auditory (Aliu et al., 2009) and tactile domains (Blakemore et al., 1999).

We estimated the readiness potential mean amplitudes for each subject within a time window of 500–100 ms before the button press and obtained an individual index of the motor-induced modulation of visual perception by computing the difference in accuracy between the short and long ASIs. The correlation between these two measures showed higher visual sensitivity around the time of action execution in participants with larger readiness potential amplitudes. Although earlier studies have related the readiness potential to confidence (McAdam and Rubin, 1971) and sensory anticipation following a
self-initiated movement (Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018; Travers et al., 2021), ours is the first study to implicate the readiness potential directly in visual sensitivity. McAdam and Rubin (1971) reported that the amplitude of the readiness potential is associated with confidence in perception of a visual stimulus presented right after the depression of the switch. They found that when participants were certain about the visual percept, their readiness potential was more negative then when they were doubtful or ambivalent about it. Their results were limited to visual stimuli presented with a fixed and predictable delay after the action, and the reported association might be mediated by cognitive processes and decision mechanisms. Our result shows that sensitivity, a signature of early visual processes, is associated with the amplitude of the readiness potential preceding the action and, more importantly, interindividual differences in readiness potential amplitudes recorded in a condition without visual stimulation are predictive of the magnitude of the individual perceptual modulation. This suggests that the amplitude of the readiness potential response is associated with a modulation in visual sensitivity around the time of action execution, and it predicts, even in the absence of visual stimuli and tasks, the magnitude of this modulation within each participant. This is consistent with recent fMRI findings with a similar task design, showing that primary visual cortex is rhythmically suppressed as a function of visual stimuli ASI from action onset (Benedetto et al., 2021).

Is the modulation of visual accuracy following a button press a form of motor-induced suppression, similar to that observed during saccadic eye movement (i.e., saccadic suppression)? The modulation reported here and saccadic suppression differ in at least one aspect. The magnitude of the modulation (~5%) is not comparable to the suppression that is associated with saccadic eye movements. Saccadic suppression is much stronger, causing a complete phenomenological ablation of the visual input. Evidence suggests that saccadic suppression mostly derives from a selective suppression of the magnocellular visual pathway (Burr et al., 1994), mediated by a corollary discharge signal that changes the gain of the visual responses (Diamond et al., 2000; Ross et al., 2001; Binda and Morrone, 2018). The function of this suppression may be related to the selective suppression of the spurious motion signals generated by the eye movement (Burr et al., 1982). Whether the motor-induced suppression beyond the oculomotor system has the same function is less clear, as other types of movements (e.g., button press) may not induce similarly spurious visual signals. However, these movements can give rise to cross-modal interactions, and the small visual suppression we report may relate to the attenuation or recalibration of this cross-modal effect (Alais et al., 2010). For instance, saccades can affect auditory (Krüger et al., 2016; Gruters et al., 2018) and tactile (Harrar and Harris, 2009) perception. Similarly to our results, these cross-modal effects are less strong than the intramodal ones (Harris and Lieberman, 1996), leaving open the possibility that the modulation reported here may reflect a mechanism of motor-induced suppression.

Although the exact nature of readiness potential is still under debate (Schurger et al., 2021), a number of studies have shown that the readiness potential amplitude is modulated by sensory expectation (Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018; Travers et al., 2021). It is well know that temporal expectation modulates visual performance over time (Nobre et al., 2007). For instance, Fiebelkorn et al. (2013) measured visual detection at several delays from the appearance of a visual cue. They found that detection rate increased with the cue-to-target delay. It has been argued that (pre)motor modulations may be confounded with attentional/anticipatory processes (Hughes et al., 2013; Stenner et al., 2014a, b). Although our study does not address this question, Stenner et al. (2014a) showed that visual accuracy, after controlling and accounting for stimulus predictability (i.e., sensory expectation) and motor output (i.e., motor prediction), was still reduced to self-generated visual stimuli. Interestingly, they also found enhanced prestimulus activity (7.5–12.5 Hz) in the visual cortex when the identity and onset of the stimulus are controlled by participants’ motor actions. Activity is typically associated with neuronal inhibition (Klimesch et al., 2007; Jensen et al., 2012), and prestimulus activity has been shown to predict visual detection accuracy (Busch et al., 2009). Stenner and colleagues interpreted the prestimulus activity in their study as a signature of sensory anticipation and attenuation induced by the movement (Stenner et al., 2014a).

The modulation of visual accuracy reported here might be influenced by (or reflect) a combination of different processes including motor actions, perception, and temporal predictions. Nevertheless, it is noteworthy that readiness potential in the motor-only task predicted the magnitude of the modulation of visual accuracy, although participants performed no visual task in that condition with no allocation of attention or visual expectation resources. Therefore, the correlation between the readiness potential and the differences in peri-action perception might also reflect the activity of temporal coordination of action and perception. This coordination is achieved by establishing a precise sensorimotor synchronization around the time of action execution. This is consistent with evidence showing an association between the readiness potential dynamics and temporal recalibration of cortical activity after adaptation to altered visuo-motor temporal delays (Cai et al., 2018). Furthermore, the readiness potential has also been linked to intentional binding, which relates to the perceived time of sensory outcomes following a voluntary action (Jo et al., 2014).

Could this sensory-motor temporal coordination mechanism rely on efference copy signaling (Engel et al., 2001; Melloni et al., 2009)? Intriguingly, intentional binding is considered critical for developing a normal sense of agency, that is, the experience of controlling action to influence events in the environment (Moore and Obhi, 2012). Both sense of agency and intentional binding are thought to be impaired when efference copy signaling is dysfunctional, such as in schizophrenia and autism (Feinberg, 1978; Shergill et al., 2005; Ford et al., 2014; Yao et al., 2021).
These impairments may be also associated with abnormal readiness potential amplitudes (Feinberg, 1978; Ford et al., 2014; Yao et al., 2021) and sensory attenuation for self-triggered stimuli (Shergill et al., 2005). Given these associations, the correlation that emerged from the current study might provide an interesting tool for studying intentional binding and sense of agency in individuals with different personal traits (e.g., schizotypical and autistic).

Although controversial (Wilke and Lansing, 1973; Hazemann et al., 1978), biophysical factors related to the preparation of specific movements, such as motor coordination and force, may also modulate the readiness potential (Ford et al., 1972; Kutas and Donchin, 1974; Becker and Kristeva, 1980; Kristeva et al., 1990). As we did not record participants’ kinematics, we cannot exclude the possibility that differences in the readiness potential amplitude across participants are because of differences in movement performance. Although visual suppression is known to increase with larger saccade and blink amplitudes (Volkmann et al., 1981; Stevenson et al., 1986), it is unclear whether this is also true for body movements, including the force of the button press. Therefore, the exact relationship of movement force to readiness potential amplitude and motor-induced visual suppression may need to be considered in future studies.

Our task required a fine visual discrimination which would have been strongly affected by failures to maintain central fixation and – in particular – by blinks (Volkmann, 1986). Therefore, the motor-induced modulation of visual perception we report here could also be explained by a difference in the probability of blink occurrences between the short and long ASIs conditions. However, our analysis suggests that blinks around the button press were rare (see Extended Data Figs. 1-2 and 1-3), implying that participants only tended to blink long after the stimulus presentation. Therefore, blinks are unlikely to account for the observed suppression in accuracy. Similarly, saccadic eye movements can also impact visual accuracy (Volkmann, 1986; Burr et al., 1994). However, in our paradigm, visual stimuli were randomly displayed on the left or right side of the monitor, which would favor central fixation as optimal strategy for better discrimination. We also used very brief stimuli that could have been easily suppressed during eye movement requiring, thus again, good fixation. Taken together, these observations suggest that the visual modulation reported in Figures 1 and 2 is related to the button press rather than eye movements.

In conclusion, visual sensitivity is modulated within a short time window around a voluntary action. Here, we showed that the readiness potential elicited by a button press correlates with this motor-induced modulation of visual perception, whether the action execution triggers a visual stimulus or not. This may suggest the presence of a general and automatic mechanism, possibly fundamental to establishing a precise visuomotor synchronization. Furthermore, we found that the readiness potential amplitude can predict the magnitude of individual modulation effects, which provides an interesting tool for studying normal functions and dysfunctions of visuomotor interactions in individual brains.

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