



The role of visual processing in motor learning and control: Insights from electroencephalography



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ABSTRACT

Traditionally our understanding of goal-directed action been derived from either behavioral findings or neuroanatomically derived imaging (i.e., fMRI). While both of these approaches have proven valuable, they lack the ability to determine a direct locus of function while concurrently having the necessary temporal precision needed to understand millisecond scale neural interactions respectively. In this review we summarize some seminal behavioral findings across three broad areas (target perturbation, feed-forward control, and feedback processing) and for each discuss the application of electroencephalography (EEG) to the understanding of the temporal nature of visual cue utilization during movement planning, control, and learning using four existing scalp potentials. Specifically, we examine the appropriateness of using the N100 potential as an indicator of corrective behaviors in response to target perturbation, the N200 as an index of movement planning, the P300 potential as a metric of feed-forward processes, and the feedback-related negativity as an index of motor learning. Although these existing components have potential for insight into cognitive contributions and the timing of the neural processes that contribute to motor control further research is needed to expand the control-related potentials and to develop methods to permit their accurate characterization across a wide range of behavioral tasks.

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1. Introduction

The importance of vision to motor learning and control is somewhat obvious. Indeed, the seminal work of Woodworth (1899) proposed a role for vision in all aspects of movement – planning, control, and evaluation. Following from these original ideas, a multitude of behavioral studies that have affirmed Woodworth's hypotheses and affirmed the role of vision in every aspect of motor learning and control.

Here, we review the insights provided by a recent series of studies that have used electroencephalography to examine “conscious” visual processes, and importantly the timing of said processes, that support movement planning, online control, and feedback evaluation. More specifically, we review electroencephalographic studies examining the timing of visual processing in three key areas where conscious awareness of visual events play a prominent role in motor control – movement planning, movement control, and movement evaluation. It is important to state here why we

believe using EEG and the ERP technique specifically is important in the study of the visual processes that facilitate motor planning, control, and learning. Specifically, the EEG and the ERP technique affords the ability to examine the time course of neural processing – something that is not possible to do from behavioral findings alone and is lacking in the fMRI methodology. In this review we will link the visual processes that underpin motor planning, control, and learning to four visual components of the human event-related brain potential (ERP) – the N100, the N200, the P300, and the feedback related negativity (FRN) – to provide insight into the temporal structure of these processes. We will begin our review by briefly summarizing what is known about the aforementioned ERP components.

2. A general review of visually evoked ERP components

2.1. The N100

Typically, the visual N100 component appears as a negative deflection in the ERP waveform between 125 and 200 ms following the onset of a visual cue. The N100 is typically lateralized, such that cues appearing in right visual space evoke a larger N100 at left posterior electrode sites relative to right posterior electrode sites

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and conversely targets appearing in left visual space have the mirror opposite effect – a larger N100 is evoked at right posterior electrode sites relative to the left. The N100 is typically associated with enhanced stimulus processing within a given target location and as such is related to the allocation of visuospatial attention (Harter et al., 1989; Hillyard & Anillo-Vento, 1998; Luck et al., 1990; Mangun & Hillyard, 1991). For example, the N100 has been observed during visual search tasks when a target stimulus appears in either left or right visual space. In these instances, the lateralized appearance of the target was associated with an enhanced posterior N100 response over the contralateral parietal-occipital hemisphere (Kasai, Morotomi, & Katayama, 2003; Pazo-Alvarez, Amenedo, & Cadaveira, 2004; Spironelli, Tagliabue, & Angrilli, 2006). Further, changes in the amplitude of the visual N100 have also been associated with target motion during visual search tasks (Anillo-Vento & Hillyard, 1996).

2.2. The N200

The N200 component is typically reported as a large negative modulation of the ERP waveform between 200 and 350 ms post stimulus onset. The N200 is typically subdivided into at least two subcomponents – the anterior N200 and the posterior N200. The anterior N200 was originally associated with mismatch detection but is now known to be sensitive to conflict monitoring, stimulus frequency, and aspects of language characterization (Patel & Azzam, 2005). The posterior N200 is typically seen in concordance with the posterior P300 component evoked during oddball tasks as is sensitive to stimulus frequency. The posterior N200 has also been proposed to reflect aspects of the allocation of visuospatial attention (Folstein & Van Petten, 2008). It is worth noting at this point that the N200 has been proposed to have other subdivisions related to error evaluation (FRN – see below) and attention (the N2pc) and possibly even more (Luck, 2005).

2.3. The P300

The P300 is a large, positive-going, parietally-distributed deflection in the ERP that peaks 300 ms or later following stimulus onset (Sutton et al., 1965), and is typically elicited by novel events. For example, in the “oddball task” participants respond to (or silently count) infrequently occurring target stimuli, which elicit a large P300 (Bekker, Kenemans, & Verbaten, 2005; Donchin & Coles, 1988; Duncan-Johnson & Donchin, 1977; Jackson, Jackson, & Roberts, 1999). Although the location(s) of the generator(s) that produce the P300 is not exactly clear, a number of researchers have suggested a P3 source near the temporal-parietal junction (Calhoun et al., 2006; Halgren et al., 1995; Kiss, Dashieff, & Lordeon, 1989; Knight et al., 1989; Menon et al., 1997; Molnar, 1994; Smith et al., 1990; Verleger et al., 1994; Yamaguchi & Knight, 1991, 1992). One prominent theory of the P300 holds that this ERP component indexes “context updating” (Donchin & Coles, 1988), such that it is elicited by the active updating of an internal model of the environment upon receipt of new information. More recently, the P300 has been associated with the release of norepinephrine by the locus-coeruleus to facilitate decision making (Nieuwenhuis et al., 2005).

2.4. The feedback-related negativity (FRN)

Seminal findings demonstrate that “slips” made during a speeded response task elicit a negative deflection in the ERP waveform peaking about 100 ms after error commission (the response error-related negativity: rERN; Falkenstein et al., 1991; Gehring et al., 1993). Subsequent research by Miltner, Braun, and Coles (1997) demonstrated that error feedback in trial-and-error learning tasks

elicited a similar negative deflection in the ERP that reaches maximum amplitude about 250 ms following feedback onset (the feedback-related negativity: FRN). Source localization studies of the rERN and the FRN suggests a common source for both ERP components within anterior cingulate cortex (ACC: Holroyd et al., 2004; Miltner et al., 1997; but see also Nieuwenhuis et al., 2005). Together, the rERN and FRN are proposed to be elicited by a generic error processing system evaluating, respectively, an efference copy of the motor command and external error information. Specifically, the Reinforcement Learning theory of the Error-Related Negativity (ERN) (RL-ERN theory, Holroyd & Coles, 2002) holds that the amplitude of the ERN is determined by the impact on the ACC of a reinforcement learning signal carried by the midbrain dopamine system from the basal ganglia. Further, the theory holds that the error signal is generated by the earliest indication that events are worse than expected: an rERN is elicited when the efference copy of the motor command provides the first indication that an error has occurred, and a FRN is elicited when external information provides the first information that an error has occurred (for a review see Holroyd et al., 2004).

3. The time course of conscious visual processing to support movement planning

In advance of executing goal directed actions a motor plan has to be generated that specifies the effectors and their parameters (Kawato, Maeda, Uno, & Suzuki 1990; Klapp & Erwin, 1976, Schmidt, 1975; Slater-Hammel, 1960). A key step in the generation of the motor plan is the use of an internal inverse model – a computational unit within the brain that determines the motor commands necessary to realize a desired movement trajectory – to plan an intended movement (Kawato et al., 1990). Importantly, in order for internal inverse models to generate motor plans (Bullock, Grossberg, & Guentherm 1993; Shadmehr & Mussa-Ivaldi, 1994) it is necessary for the brain to compute complex sensory-based visuomotor transformations to realize the coordinate framework necessary to execute a goal-directed movement (Kalaska, Scott, Cisek, & Sergio, 1997). These visuomotor transformations rely heavily on visual processing of target location and other environmental cues within the dorsal visual stream (Goodale & Milner, 1986, 1991). As such, vision plays a key role in movement planning as it provides key information that is needed to generate the motor plan.

Electroencephalography has been used for some time to study the temporal structure of the neural processes that underlie movement planning. Indeed, a multitude of studies have examined the Bereitschaftspotential (Shibasaki & Hallett, 2006), a motor ERP component that is thought to reflect planning related preparatory activity within the premotor and motor cortices. More recently however, electroencephalography has been used to examine the timing of the visual processes that contribute to movement planning. For instance, Praamstra, Kourtis, and Nazarpour (2009) had participants reach to several different targets while electroencephalographic data was recorded. In a key manipulation, prior to reach onset, participants were shown an instructional cue that indicated whether there were one, two, or three potential reach targets. Interestingly, Praamstra and colleagues found that viewing of the instructional cue evoked differential activity in the N200 and P300 components. More specifically, the authors found in their first experiment that the amplitude of the N200 and P300 was greater when the cue indicated multiple potential targets. In a second follow up experiment, the N200 finding was replicated and further modulation of the latency of the P300 was observed. Praamstra et al. proposed that in their experiment the modulation of the N200 and P300 was due to target selection processes within the

posterior parietal cortex and the enhancement of these components was due to the potential preparation of multiple action plans.

In a related study Kourtis and colleagues (2011) sought to determine if task difficulty impacted visual processing prior to movement onset. In this experiment the authors used electroencephalography to investigate the sensitivity of visual processes to Fitt's Law during the preparation for action. In their paradigm Kourtis and colleagues had participants perform a Fitt's Law tapping task (c.f., Fitts, 1954) while electroencephalographic data was recorded. More specifically, participants were required to tap a stylus between a series of rectangular targets that varied in width. However, prior to movement onset a visual cue appeared on a computer monitor in front of the participant that indicated the direction participants were to move – and given the experimental setup the cue also inferred task difficulty due to the differing width of the possible movement targets. Kourtis and colleagues behavioral results mirrored the classic Fitt's finding – that a linear relationship existed between movement time and index of difficulty (c.f., Fitts, 1954). In terms of the electroencephalographic results, Kourtis et al. found that the amplitudes of the N200 and P300 ERP components evoked by the cue stimulus linearly scaled to the index of difficulty of the subsequent tapping movement. The authors suggested that the N200 effects may have been related to encoding of movement amplitude and/or evaluation of the cue stimulus whereas the modulation of the P300 amplitude may have reflected an increased potential for committing an error as the task increased in difficulty (i.e., narrower targets) and/or further evaluation of the cue stimulus. As such, these data would suggest that the amplitudes of both the N200 and P300 are sensitive to the visual processing that underlies movement planning processes.

Further support for the sensitivity of the processes that underlie the generation of the N200 and P300 to movement amplitude is seen in the work of Krigolson et al. (2013). In their study, Krigolson and colleagues recorded electroencephalographic data while participants reached targets that they could see (i.e., visually-guided reaching) or to targets that they had seen but that were occluded prior to movement onset (i.e., memory-guided reaching). The behavioral findings were in line with previous accounts of memory-guided reaching (e.g., Westwood, Heath, & Roy, 2001, 2003) – participants undershot the target location in the memory-guided conditions relative to the visually-guided condition. However, the authors found that a visual cue that was presented prior to movement onset indicating whether the subsequent reaching movement would be visually or memory guided modulated the amplitude of the N200 and P300 components. More specifically, Krigolson and colleagues found that the amplitude of the N200 and P300 components were diminished for memory-guided reaches. In terms of meaning, the authors suggested that the reduced amplitude of the N200 and P300 reflected processes that resulted in the target undershooting observed in the memory-guided condition – perhaps incorrect encoding of target and/or movement amplitude.

In a different line of research examining the neural processes that sub-serve anti-pointing, Heath et al. (2012) also found relationships between the amplitude of the N200 and P300 and the encoding of reach amplitude. Specifically, Heath et al. (2012) had participants make either pro-pointing (pointing to a presented target) or anti-pointing (pointing to the mirror symmetrical target location) while electroencephalographic data was recorded. In line with previous work, participants' reach amplitudes were shorter for anti-pointing reaches relative to pro-pointing reaches (Maraj & Heath, 2010). Post experiment analysis of the event-related brain potentials evoked by an instructional cue shown to participants at the start of each trial that informed them as to whether or not they would be making a pro-pointing or an anti-pointing movement revealed that N200 and P300 amplitude was reduced for cues that indicated a

subsequent anti-pointing movement. As such, the work of Heath et al. (2012) is similar to that of Krigolson and colleagues (2013) in that it also demonstrates a relationship between the amplitude of the N200 and P300 and instructional cues that result in reaches with shorter movement amplitudes. Indeed, Heath et al.'s (2012) results, along with those of Krigolson et al. (2013) seem to suggest that the processes that underlie the N200 and P300 may be related to the encoding of target location and/or movement amplitude.

So what visual processes underlie the generation of the N200 and P300 components observed following cues that provide information about an upcoming reaching movement? And further, what does the time course of these ERP components tell us about the temporal structure of these processes? Recall that one explanation for these findings is that the processes that underlie the N200 and P300 are sensitive to task difficulty; indeed, the results of Praamstra et al. (2009) and Kourtis, Sebanz, and Knoblich (2012) support this contention. Consider the context of the Fitt's Law task – Kourtis and colleagues found that the amplitudes of N200 and P300 were linearly related to the index of difficulty for the task. But what might this mean and is it a viable explanation in terms of the N200 and P300 ERP components? As mentioned at the outset of this paper, the N200 has been shown to be sensitive to response conflict. Based on this contention, as the index of difficulty increased in the Fitt's Law task (Kourtis et al.) there will be more response conflict within the motor system and as such an increase in amplitude was seen in the N200 and P300. However, if one considers Krigolson et al. (2013) and Heath et al.'s (2012) studies, this explanation does not seem as likely. Specifically, these authors found that the amplitude of the N200 and P300 were diminished for memory-guided and anti-pointing reaches respectively. Unless one comes up with a hypothesis that there is less response conflict during memory-guided and anti-pointing reaching then it seems unlikely that the processes that underlie the N200 and P300 reflect the encoding of task difficulty.

The most likely conclusion based on the limited research to date is that the process that underlies the N200's and P300's evoked by visual cues prior to movement onset is sensitive to, or responsible for, the conscious encoding of target location and/or movement amplitude for a subsequent reaching movement. Indeed, the conclusion that the amplitude of the P300 is related to encoding of movement amplitude receives indirect support from studies demonstrating that the amplitude of the P300 is sensitive to the amount of money won or lost during the performance of gambling tasks (see Yeung & Sanfey, 2004). The fact that the N200 and P300 are attributed to cognitive processing (Luck, 2005) suggests that the neural processes that underlie these components play a conscious role in movement planning and perhaps impact the motor process in a top-down fashion and thereby target encoding and/or processing of movement amplitude. Indeed, given the prior studies that have examined the N200 and P300 in cognitive tasks (e.g., Donchin & Coles, 1988) it seems unlikely they reflect action related visual processing within the dorsal visual stream which is more typically associated with the encoding of target location and/or movement amplitude (Goodale & Milner, 1992). Finally, we will emphasize here that the modulation of these components also provides insight into the timing of the conscious contributions to the encoding of target location and/or movement amplitude. Specifically, in sum the aforementioned studies suggest that conscious contributions to the visual encoding of target location and/or movement amplitude take at least 200 to 300 ms to process.

4. The timing of conscious visual processing during online control

In addition to movement planning, visual processing also plays a key role in the online control of movement; providing

information that allows the motor system to adjust an ongoing action or accommodate an unexpected change in the movement environment (Chua and Elliot, 1993; Desmurget et al., 1999; Elliott, Helsen, & Chua, 2001; Goodale & Milner, 1992; Keele & Posner, 1968; Meyer et al., 1988; Milner & Goodale, 1993, 1995; Westwood & Goodale, 2003; Westwood et al., 2003). For example, Keele and Posner (1968) examined the time course of visual processing during the online control of movement. Specifically, they manipulated the availability of visual feedback for participants reaching to a series of target locations by changing the availability of light in the experimental room. Further, to examine the time course of visual processing Keele and Posner also required participants to complete their reaching movements within four different movement time bandwidths. Interestingly, they found that extremely rapid reaching movements (movement times less than 190 ms) were as accurate as reaches made without the availability of visual information (e.g., in the dark). However, movements that were completed with movement times greater than 260 ms were more accurate than their faster and no-vision counterparts. From these findings they concluded that the availability of vision during reaching movements did facilitate accuracy – however, there was a minimum amount of time that was needed to be able to utilize this information – from their data about 190 to 260 ms. These findings affirmed the notions of Woodworth (1899) who had proposed a two-component model of reaching that included both a ballistic pre-programmed phase and a secondary online control phase. To emphasize this finding – the importance of Keele and Posner's work was that it was the first attempt to try and quantify the minimum amount of time needed to utilize visual information to improve movement accuracy and/or nullify errors in the initial motor command. Since the work of Keele and Posner (1968) there have been a multitude of studies that have affirmed the role of visual feedback in the online control of movement and further examined the time course of visual processing during online control (e.g., Elliott et al., 2001; Glover & Dixon, 2001a, 2001b; Glover & Dixon, 2002a, Glover, 2002b; Heath, 2005; Heath et al., 1998; Krigolson & Heath, 2004; Meyer et al., 1988; Milner & Goodale, 1993, 1995; Westwood & Goodale, 2003; Westwood, et al., 2003).

4.1. Conscious visual processing of target perturbations

One of the more common methods of inducing online control directly is by experimentally perturbing the either the target or the limb during the execution of an aiming movement (e.g., Cameron et al., 2013; Mistry et al., 2013). Correspondingly, Krigolson and Holroyd (2007a) directly examined the electroencephalographic correlates of the visual processing associated with such target jumps. Specifically, they had participants manipulate a joystick to rapidly move a cursor from a start to a target location within the context of a computer based aiming task while EEG data was recorded. Unbeknownst to participants, on some trials the movement target would make an unexpected vertical “jump” in target location during the execution of their aiming movements after movement onset. The perturbation forced participants to make an online adjustment to their aiming movement by engaging online control processes and manipulating the joystick to accommodate the target perturbation. In a further manipulation, on one half of the perturbation trials, any attempt at a corrective movement was blocked by computer aiming program thus negating a participants ability to make a corrective sub-movement. These manipulations revealed that unexpected changes in target location evoked two prominent responses in the event-related potential (ERP) waveforms. Specifically, the average EEG response to the target jump revealed a lateralized posterior component peaking approximately 150 ms post target jump, the N100, and a

later midline parietal component peaking approximately 300 ms post target-jump, the P300 (see Fig. 1).

As noted above, the N100 observed by Krigolson and Holroyd (2007a) peaked shortly after the onset of the target perturbation and had a maximal component amplitude over left parietal-occipital visual areas of cortex (see Fig. 2). Given the timing of the N100 observed, and with Keele and Posner's results in mind, Krigolson and Holroyd posited that the potential was too slow to simply reflect the arrival of visual information in primary visual cortex. Further, the timing and scalp distribution of the ERPs were consistent with the aforementioned accounts of the N100 observed during the performance of visual search tasks. Given that all of the target perturbations occurred in the right visual field, they proposed that the left lateralized N100 component reflected the detection of the target perturbation by early visual processes associated with the allocation of visuospatial attention. Importantly, the timing of the N100 was similar to the minimum time believed to be required for feedback-reliant control processes (Desmurget & Grafton, 2000; Jeannerod, 1988; Keele & Posner, 1968; Paillard, 1996) and as such they concluded that the N100 may be related to the visual processing that supports the online control of movement. In other words, the N100 elicited by target perturbations may reflect neural activity associated with a more advanced stage of visual processing – one that facilitates efficient motor control such as the detection of unexpected environmental change, the magnitude of the change, and/or the location of the change (cf. Milner & Goodale, 1993).

Interestingly, in the Krigolson and Holroyd study the timing of corrective sub-movements occurred during the offset of the N100 component. As such, the conscious processing of the target perturbation as evidenced by the timing of the N100 component could be a precursor to online control and associated with the updating of target location within visuomotor areas of cortex – a proposal, which if true, is in opposition to the original “silent” and unconscious role of the dorsal visual stream (e.g., Goodale & Milner, 1986, 1991). While the time course may seem short, it is important to realize that given the nature of determining onsets and offsets for event-related brain potential components the authors were unable to analyze this key finding – the time course of the N100 relative to corrective changes in reach trajectory – at an individual level. As such, it remains unclear whether or not these two processes, the N100 and corrective sub-movements, are directly related. Importantly however, the timing of the N100 at least provides a minimal window of time that is needed to consciously process a change in the movement environment and reallocate the focus of visuo-spatial attention accordingly.

Sadly, to date, there is little work other than these few studies that has used electroencephalography to examine the processing of unexpected environmental changes during the online control of movement and as such the relationship between the N100 and the processing of target perturbations is still unclear.

4.2. Feed-forward control

While it seems clear that visual feedback is necessary to make online movement amendments, vision alone is not sufficient to achieve movement accuracy. If online control processes were to rely solely on visual and/or proprioceptive feedback then the online corrective movements would be subject to a sensory processing delay of at least 80–100 ms (see above; and see Jeannerod, 1986; Paillard, 1996). To solve the delay problem, at least for internally generated errors, it has been proposed that the motor system takes advantage of a predictive forward model that utilizes an efference copy of the motor command to estimate future movement states in advance of their occurrence. If one then places the forward model within an internal closed feedback loop,

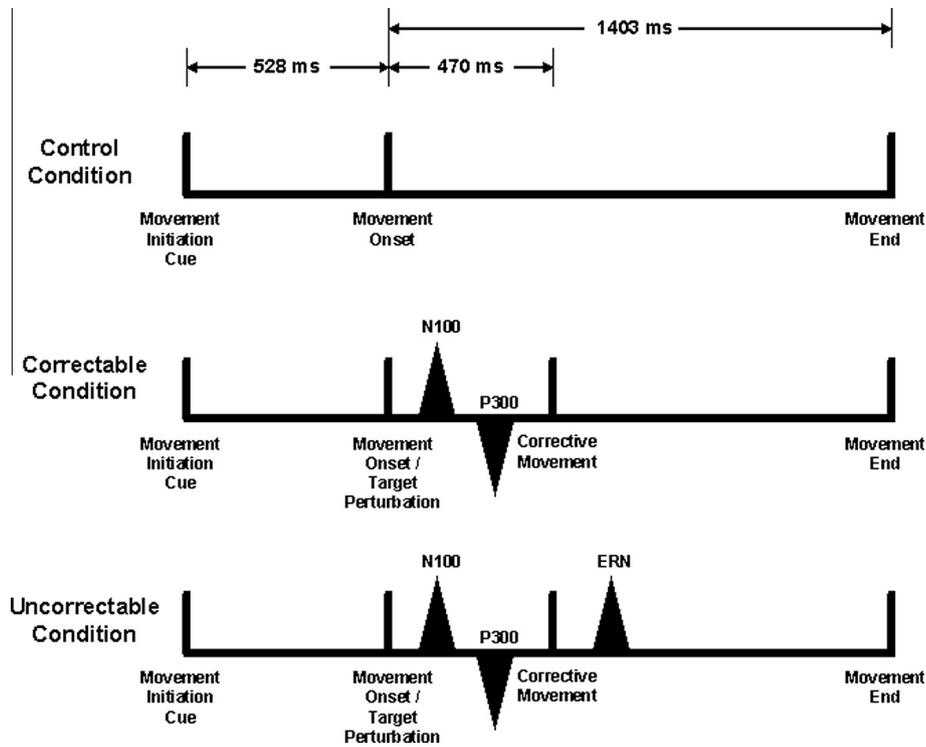


Fig. 1. The time course of ERP components elicited by target perturbations in Krigolson and Holroyd (2007d). Note that the N100 and P300 in this experiment after the target perturbation but before the corrective movement.

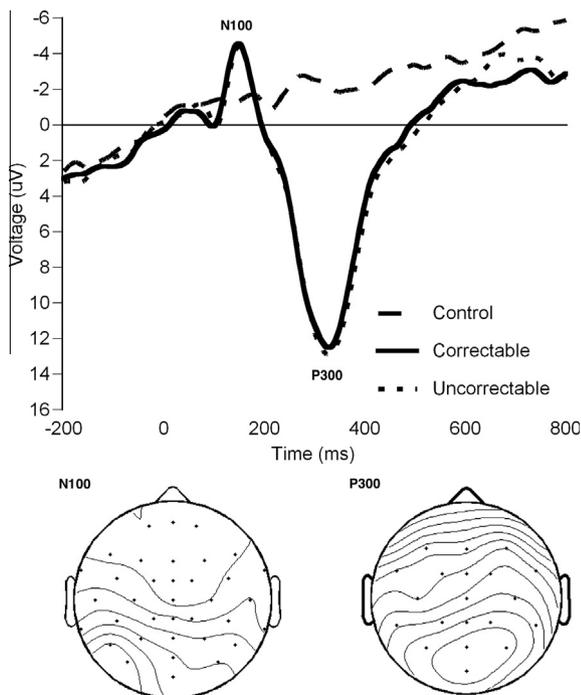


Fig. 2. The ERP waveforms and the ERP components with their associated scalp topographies evoked by target perturbations. The target perturbation occurred at 0 ms relative to this plot. Note that negative is plotted upwards by convention.

the system can act on the predictive information before it actually occurs, thus negating the sensory feedback delay (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000). But how would a forward model learn to make accurate predictions? For a forward model to be effective in principle it would need to learn the task

constraints, the environment, and of course the consequences of motor commands on a given movement effector. Thus, it stands to reason that while a movement is underway, two streams of information need to be processed – information that will be utilized within the ongoing movement to achieve movement accuracy and information that is already being signaled “ahead” to be utilized to improve the performance of subsequent actions (i.e., improve forward models).

4.3. Feed-forward control: the timing of conscious visual processing

In addition to their observations regarding the underpinnings of online control, Krigolson and Holroyd’s (2007d) also demonstrated that target perturbations elicit a P300 ERP component – a component with a midline parietal scalp topography that peaked approximately 350 ms after the target jump (see Fig. 2). Interestingly, the timing of the P300 component in this study suggested a possible role in mediating online control processes, a contention further supported by the parietal scalp topography – a result in line with Goodale and Milner (1991, 1986) localization of the dorsal visual stream and more recent work by Desmurget and colleagues (2000) amongst others.

In a follow up study, Krigolson and colleagues (2008) replicated Krigolson and Holroyd’s (2007d) paradigm but instead utilized a rapid goal-directed aiming task as opposed to a joystick aiming task. One of the key manipulations in this study was aiming speed – participants were forced to complete their aiming movements with movement times between 400 and 600 ms, considerably faster than in the original work done by Krigolson and Holroyd (2007d). The results of the 2008 study revealed that participant’s corrective movements began before the onset of the P300 component, thus negating a possible direct role of the P300 in online control. However, the occurrence and timing of the P300 did not rule out the possibility that it played a key role in a feed-forward process. Indeed, it stands to reason that information about the target

perturbations – timing, amplitude, direction, etc – would be of critical importance for the optimization of the internal models that underlie online control. As such, the conscious processing of the target perturbation – in this instance in a feed-forward manner – apparently plays a crucial role in the online control of movement.

As with the N100 results outlined above (i.e., Krigolson & Holroyd, 2007d), it should not be surprising that the target perturbations elicit a P300, as it is normally elicited by unexpected task-relevant events (Donchin & Coles, 1988). Nevertheless, Krigolson and Holroyd's original results were brought into question by subsequent work (i.e., Krigolson et al., 2008) and the role of the P300 in online control seems unlikely now. However, the new data (Krigolson et al., 2008) provided insight into a potential role of the mechanism underlying P300 generation in feed-forward control. It is interesting to note that an important aspect of rapid motor control involves comparing the consequences of the current motor command to the movement's desired end-state (e.g., Bullock et al., 1999; Desmurget & Grafton, 2000). To do so, the system must continuously predict the outcome of the current motor command while simultaneously monitoring the external environment for changes that would negate its effectiveness. This process entails the development and execution of an internal forward model of the environment that must be updated in response to unpredicted events. Given that the context-updating hypothesis proposes that the P300 is elicited by just such an occurrence (Donchin & Coles, 1988), and given the proximal location of the temporal-parietal junction to PPC, and finally given the relatively "slow" timing of the P300 component (~400 ms post target perturbation) observed by Krigolson and colleagues (2007, 2008) we speculate that the P300 in this task may index the revision of an internal forward model by posterior cortex and thus may reflect part of the online control process.

Further evidence highlighting the role of parietal ERP components in feed-forward control is provided by an earlier study by Hill and Raab (2005). In their study, the authors examined the ERP components evoked during performance of a complex tracking task. However, unlike the aforementioned findings, after corrective movements Hill and Raab observed a centro-parietal negativity that they attributed to feed-forward related modifications following error commitment. While the time course of the component they observed was similar to the P300 (approximately 400 ms) the opposite polarity suggests the component they observed was not the P300 but instead a different component. Indeed, given that in the Hill and Raab study, the visual processing was not an environmental change (e.g., a target perturbation) but instead was due to self-evaluation of error it stands to reason that the component they observed was not as previously stated a P300. Instead of being related to a feed-forward control process the component Hill and Raab observed was most likely related to error evaluation as the authors claimed – perhaps the feedback related negativity (Miltner et al., 1997: peaking typically at approximately 250 ms) or the N400 (Kutas & Hillyard, 1980: peaking typically at 400–500 ms). While the timing and topography are not consistent with previous accounts of the FRN (Miltner et al., 1997), some researchers have found that the timing of the FRN can be considerably later when visual feedback evaluation is complex in nature (see Krigolson et al., 2013 for more detail). As such, we suggest that in this instance the component observed by Hill and Raab was related to motor learning (see next section) as opposed to motor control.

5. Visual processing and motor learning

In addition to the aforementioned roles of conscious visual processing in motor control, the processing of visual information at a

cognitive level also plays a key role in motor learning – also a necessary feature of successful goal-directed movement. Since the work of Adams (1971) it has been well established that the processing of visual feedback is a critical component of motor learning – indeed, the notion of error driven learning is not new (Wolpert, Diedrichsen, & Flanagan, 2011). Indeed, the basic notion of reinforcement playing a role in the adaptation of behavior has been with us formally since the seminal work of Thorndike (1911) with his Law of Effect: the law posits that actions that are reinforced will be repeated and that actions that are punished will be discontinued. Reinforcement learning is driven by the computation of prediction errors – the discrepancy between an actual and an intended outcome (Bennett & Castiello, 1994; Jordan & Rumelhart, 1992). Importantly, the reinforcement learning problem is the exact situation encountered in motor learning and control – after finishing a movement we compare the observed outcome with the intended one and attempt to modify behavior. Relevant to this review, the processing of visual feedback is essential for this process – we need to use vision to see our intended outcome (the target) and also see the actual outcome (the position of our limb relative to the target). Here we will review studies that have used electroencephalography to examine the visual contributions to the modification of behavior.

5.1. Post movement processing of visual feedback: the feedback error-related negativity

In line with reinforcement learning theory, studies that have used electroencephalography to examine motor learning have found that visual observation of a movement error elicits an ERP component with a timing and topography consistent with the FRN. For instance, in an early study examining this issue Krigolson and Holroyd (2006) had participants perform a continuous computer tracking task in which they attempted to keep a cursor centered between two moving barriers. In this task an error was defined as contact between the cursor and either of the barriers – an event that had to be processed visually. Krigolson and Holroyd found that tracking errors (cursor – barrier contact) elicited a negative deflection in evoked potential, with a latency and scalp distribution consistent with the FRN (see also Krigolson & Holroyd 2007b, 2007c). In terms of interpretation, Krigolson and Holroyd proposed that the medial-frontal reinforcement learning system proposed by Holroyd and Coles (2002) was sensitive to errors in continuous motor tasks. In other words, Krigolson and Holroyd suggested that a generic reinforcement learning system within the medial-frontal cortex was also responsible for at least some aspects of motor learning.

Testing this proposition, Krigolson and Holroyd (2007d) and Krigolson et al. (2008) had participants evaluate visual feedback that indicated the success or failure of a given movement during performance of a goal-directed aiming task. In the 2007 paper, Krigolson and Holroyd included a condition where corrective movements to accommodate target perturbations were blocked. An analysis of the cortical response evoked by the blocking of corrective movements revealed a FRN component similar to that observed by Krigolson and Holroyd (2006, 2007b, 2007c) – a result the authors posited was brought about because blocking the movement prevented the attainment of the movement goal. From a reinforcement learning perspective this makes sense – the blocking of the corrective movement provides a situation when the intended and actual outcomes do not align and thus a prediction error should be computed. Given that the FRN is thought to reflect a reinforcement learning prediction error (Frank, Woroch, & Curran, 2005; Holroyd & Coles, 2002; Holroyd & Krigolson, 2007; Krigolson, Hassall, & Heath, 2014), it stands to reason that one would be observed when corrective movement are blocked.

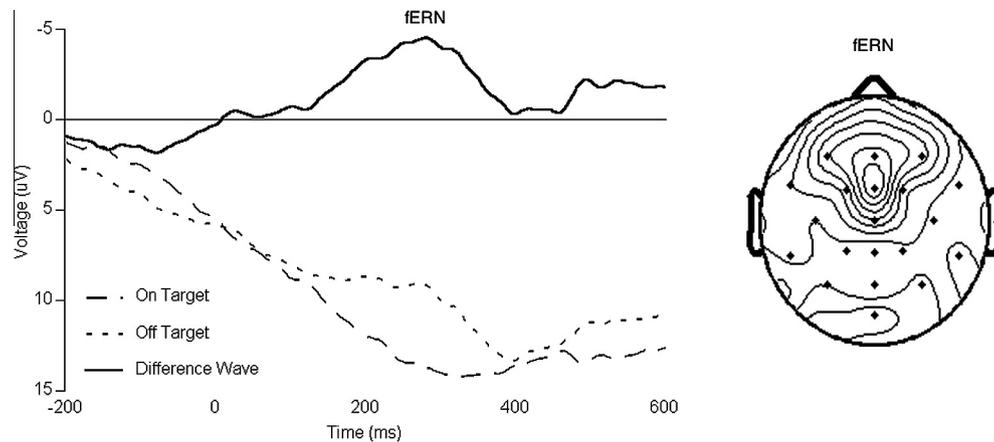


Fig. 3. A comparison of hit and miss waveforms in a goal-directed aiming task showing the feedback error-related negativity. Note that negative is plotted upwards by convention.

In another study, Krigolson and colleagues (2008) were able to demonstrate that the evaluation of endpoint error – missing a movement target – also elicited a neural response akin to the FRN (see Fig. 3). Here, participants made rapid aiming movements to a target location and due to the nature and speed of the task, on some trials they missed the movement target. A comparison of the grand-average on target and off target waveforms revealed a component with a timing and topography similar to that of the FRN. Later work by Anguera, Seidler, and Gehring (2009) extended this further. In their paradigm, participants also made rapid aiming movements to target locations. However, in an important post-experiment analysis the authors analyzed the FRN with regard to the degree to which participants missed the target location. Interestingly, Anguera et al. found that larger FRN amplitudes were associated with larger degrees of endpoint error and conversely smaller FRN amplitudes were associated with smaller degrees of endpoint error. This is a key result as it suggests that the error signal reflected by the FRN during the evaluation of endpoint error is sensitive to the magnitude of the error. If the FRN is reflective of a reinforcement learning system that drives motor learning with would be a crucial piece of information to encode. Thus in sum, all of the studies reviewed in this section suggest that motor learning may be the province of a generic reinforcement learning system within the medial-frontal cortex and that the visual processing of feedback by this system following movement errors is reflected in the FRN and leads to motor learning.

5.2. Conclusions

In sum, our review has highlighted the seminal behavioral findings relating to the processing of target errors (i.e., target perturbations – changes in the movement environment) and outcome errors (i.e., failing to achieve a movement goal). We have extended our review by discussing more recent studies that have used electroencephalography and specifically event-related brain potentials to highlight the impact of the conscious processing of visual cues on motor control. Importantly, the reviewed electroencephalographic studies provide key insight into the temporal structure of the visual processes that support movement planning, control, and learning.

The studies reviewed here demonstrate that conscious processing of target location and/or the encoding of movement amplitude is reflected in changes in the amplitude of the N200 and P300 ERP components. As such, the ERP evidence suggests that conscious contributions to movement planning brought about by the processing of visual cues – such as target presentation – occur

relatively slowly, starting at least 200 to 250 ms after cue onset. In terms of target perturbations, our review highlights that the N100 component appears to reflect the reallocation of visuo-spatial attention to a new target location, and its timing is in line with seminal work by Keele and Posner (1968) that determined an initial estimation of the initial amount of time needed for the processing of visual information for online control. We have also reviewed work that suggests that the visual P300 component evoked by target perturbations may be related to feed-forward control processes. The reviewed ERP research also examines the FRN, an ERP component evoked by outcome errors that has been hypothesized to play a key role in motor learning.

However, there remain a number of barriers that limit the application of EEG in general and ERP methodologies in particular to the study of motor control. First, there is a paucity of identified peaks that have direct relevance to movement control. Although we have reviewed four existing ERP components, potentials related to critical behavioral features such as discrete/continuous online corrections need identification and characterization. Second, despite recent advances in decomposition techniques, the dominating presence of the motor related cortical potential acts as a significant obstacle to identifying small peaks. This potential is large, time-varying, and spans duration of movement preparation through control. Whether by variants on decomposition, wavelets, or other techniques, a consensus solution needs to be arrived at on how to identify peaks within a movement. Third, and perhaps most importantly, to date there are no known ERP components associated with processing by the dorsal visual stream (c.f., Goodale & Milner, 1992). As such, all of the work here reflects conscious visual processing of visual cues that impact motor planning, control, and learning. More work needs to be done to identify whether or not there are “dorsal stream ERP components”, what they are, and what processes they reflect.

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