RESEARCH ARTICLE

A perception-based ERP reveals that the magnitude of delay matters for memory-guided reaching

Leanna C. Cruikshank · Jeremy B. Caplan · Anthony Singhal

Received: 9 December 2013 / Accepted: 25 February 2014 © Springer-Verlag Berlin Heidelberg 2014

Abstract Delayed action research has suggested that perceptual information about a visual stimulus decays over several seconds. With event-related potential (ERP) methodology, one should be able to track the time course of the electrophysiological processes associated with this decay. Recently, Cruikshank et al. (J Vis 12:29, 2012) found that the N170 ERP component reflected ventral stream processes linked to motor planning and perception for action. Specifically, the N170 was larger for actions that relied on perceptual-based information. However, the delay interval was very short (tens of ms). Behavioral and neuroimaging studies suggest that when longer delays are employed, reactivation of ventral areas is necessary in order to access a stored representation of the target's characteristics. Therefore, the N170 may reflect not only the perceptionfor-action processes, but also the accuracy of the representation. In order to test this, we traced the time course of the N170 in memory-guided reaching when 1-, 2-, and 3-s delays separated target occlusion and response initiation. During reach initiation, the N170 was more negative and peaked earlier for the 1 s than the 2- and 3-s delays and correlated significantly with performance at the longest delay. These results suggest that the neural mechanisms involved in movement planning change for delays beyond 1 s. The smaller N170 may reflect an impoverished visual perceptual representation in the ventral stream. To our knowledge, these are the first electrophysiological results to suggest that there is decay of visual perceptual information that occurs with increasing time.

Keywords Memory-guided action \cdot Event-related potentials \cdot N170 \cdot Perceptual memory

Introduction

The role of vision in goal-directed movement has important implications for how motor behaviors are planned and executed. When continuous visual input is available, dorsal stream mechanisms in the posterior parietal cortex are thought to compute sensorimotor transformations at the time a response is cued (Goodale and Milner 1992; Westwood and Goodale 2003). Thus, visually guided movements are thought to unfold in real time and are supported by online control processes (Elliott et al. 2001). Instead, when visual input is unavailable, or vision is occluded at the time a response is cued, a stored perceptual representation must be used instead to inform the motor plan. Under such memory-guided conditions, mechanisms in the ventral stream, particularly those associated with inferior temporal cortex, are engaged (Goodale 1998). Converging neuropsychological, neuroimaging, and kinematic findings support this theory (Goodale et al. 1994; Hu and Goodale 2000; Westwood et al. 2000, 2001; Singhal et al. 2006; Ganel et al. 2008; Cohen et al. 2009). There is ample evidence arguing against a double dissociation between vision for action and vision for perception, however, as many studies have also suggested that the dorsal stream is engaged for

L. C. Cruikshank (☒) · J. B. Caplan · A. Singhal Centre for Neuroscience, University of Alberta, 5005-A Katz Group-Rexall Centre, Edmonton, AB T6G 2E1, Canada e-mail: leannac@ualberta.ca

J. B. Caplan e-mail: jcaplan@ualberta.ca

A. Singhal e-mail: asinghal@ualberta.ca

J. B. Caplan · A. Singhal Department of Psychology, University of Alberta, P217 Biological Sciences, Edmonton, AB T6G 2E9, Canada

Published online: 02 April 2014



actions in which vision of the target is unavailable (Franz et al. 2009; Hesse and Franz 2009). This position is supported by monkey neurophysiology and human fMRI data, which reveal that sustained activity occurs in dorsal parietal neurons across memory delays (Murata et al. 1996; Buneo et al. 2002; Singhal et al. 2006; Fiehler et al. 2011; Himmelbach et al. 2009). It is likely that while the ventral stream is necessarily engaged for memory-guided action, collaboration between the two streams also occurs and depends on the specific requirements of the task (Schenk and McIntosh 2010).

Recently, we provided the first event-related potential (ERP) evidence that action planning in the absence of a visual target engages ventral stream processes, making it possible to investigate the electrophysiological basis of goal-directed reaching. Specifically, the N170 ERP component, which is an established marker of ventral visual stream processing, was enhanced for actions that relied more heavily on perception-based information (Cruikshank et al. 2012). The N170, which was first described and widely studied in the context of face perception (Eimer and Holmes 2002; Batty and Taylor 2006; Eimer 2011; Wronka and Walentowska 2011), is also elicited in response to visual stimuli (Bentin et al. 1996), reflects the early classification of objects (Rossion et al. 2003; Sreenivasan et al. 2007), is modulated by memory (Morgan et al. 2008; Banko et al. 2009), and has a known source in the lateral occipital cortex (LOC) (Rossion et al. 2003), part of the ventral visual stream. We found that N170 was enhanced for actions that relied more heavily on perception-based information (Cruikshank et al. 2012); it was larger (more negative) when the target disappeared just before reach initiation (simultaneously with the auditory cue to respond) than when it persisted until movement onset (when the participant initiated a reach). Because participants could not make a 0-ms response, the brief maintenance and recall process in both conditions of our task necessitated perceptual activity in ventral stream brain areas. However, the differential contribution of this activity was reflected in the N170 range amplitude. This ERP may arguably have been a visual N1, as this component is also elicited in response to visual stimuli, arises from the LOC, and it may not be distinct from the N170. Nevertheless, the results of Cruikshank et al. (2012) suggest that the negativity is an index of ventral stream processing during the planning of actions that rely on perception-based information. In that study, however, the memory-guided reach initiation occurred only milliseconds after the target stimulus disappeared. In this study, we considered what might happen with longer delays.

We measured EEG during a memory-guided reaching task, and the N1/N170 range ERP was computed off-line at the time of response cueing following 1-, 2-, and 3-s

delays. In order to retain the same nomenclature used in Cruikshank et al. (2012), we will refer to this component as the N170. While our initial ERP results were consistent with earlier studies assessing ventral stream activity during very short delay periods (Westwood and Goodale 2003; Singhal et al. 2007), other studies have employed much longer delay intervals between stimulus occlusion and response initiation (Hu and Goodale 2000; Milner et al. 2003; Singhal et al. 2006, 2013). Neuroimaging has shown that that the LOC is activated in response to a target stimulus, returns to baseline levels of activity, and is reactivated with the cue to respond. The suggestion is that dorsal stream mechanisms plan and maintain an action; however, at the time a response is cued, motor programming requires reactivation of detailed visual perceptual information in the ventral stream (Singhal et al. 2013). It has also been suggested that as the time interval in delayed action tasks increases, perceptual information about the visual stimulus decays (Glover 2004). While it is clear that delayed action re-recruits the LOC (Singhal et al. 2013) and that this area is necessarily implicated in delayed, compared to immediate action tasks (Cohen et al. 2009), it is unclear how the integrity of the stored perceptual information is represented. By measuring the N170 at the time of response cueing in our task, we tested whether the negativity reflects reactivation of a stored percept or whether it is simply associated with early planning and residual stimulus processing following very short delays. If the N170 is only associated with early planning and processing of the stimulus that precedes movement programming, there should be no difference in its characteristics across different delay periods of a memoryguided reaching task. That is, we would only expect to notice changes in its morphology depending on whether a target stimulus was either present or absent at the time of response cueing; the length of time a target had been occluded prior to the reach would not have any bearing on whether or not the ventral stream was engaged at movement initiation. If, however, the N170 reflects reactivation of a visual percept, then the increased memory demands associated with longer delay periods should affect the stored representation and consequently the morphology of the N170. As time elapses and visual memory is increasingly taxed, we would expect to see this process reflected in the amplitude and latency of the N170.

In sum, we tested whether the same ventral stream processes were engaged and reflected by the N170 when visual memory was taxed beyond a few hundred milliseconds. We traced the time course of the N170 in memory-guided reaching over longer delays in order to determine how perception for action is controlled over time and whether the requirements for perceptual processing are the same for longer, as they are for shorter delays.



Materials and methods

Participants

Thirty (16 female) right-handed undergraduate students, aged 17–29 (mean 20 years, SD 2.8 years), received psychology course credit for participating in this study. Three participants' data were excluded from the analyses due to persistent EMG contamination. All participants had normal or corrected-to-normal vision and normal hearing. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board and the Declaration of Helsinki.

Procedure

The study was conducted in a darkened, electrically shielded, and sound-attenuated chamber. At the start of the experiment, participants were seated in front of a 430.4 mm \times 270.3 mm touch screen. At the beginning of each session, the touch screen was recalibrated by the participant being tested to ensure that accuracy measures remained reliable across subjects. Based on the average distance from the screen (51.4 cm), the horizontal and vertical visual angles of the touch screen were 45.44° and 29.46°, respectively. The horizontal and vertical visual angles of the stimuli were 1.00° and 1.56°, respectively.

Our task required that participants reach toward and touch 9 mm \times 14 mm black dots displayed on the touch screen using E-Prime presentation software version 2.2 (Psychology Software Tools). The participant depressed a button to begin each trial. One second after the button was depressed, a target appeared on the screen in a random location, which the participant was told to fixate on. The target remained on the screen for 1,500 ms, after which it was extinguished and a blank screen remained for a delay

period of either 1, 2, or 3 s. Following the delay, an 800 Hz, 64 dB (SPL) tone sounded for 50 ms. The participant was instructed to continue holding down the button until he/she heard the tone and then to touch the target as quickly and accurately as possible. After participants made contact with the screen, they were to return their finger to the response box and hold down the button, which advanced the next trial after 1 s (Fig. 1). Prior to testing, ten practice trials were administered to ensure that participants understood the task. The 1-, 2-, and 3-s delay periods were presented randomly, and a total of 360 test trials (120 per condition) were included in a session. Participants were given a self-paced break period every 120 trials.

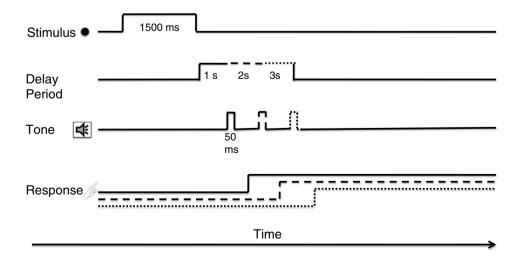
Behavioral analyses

For each trial, reaction time (RT) and movement time (MT) were recorded. RT was defined as the time it took to initiate a movement in response to the beep, and MT was defined as the time it took to fully execute a movement, from release of the response button to contact with the touch screen. Touch positions were monitored, and absolute error (pixels/mm) was recorded for each trial. Trials were excluded from analyses if RT was ≤ 150 or ≥ 800 ms or MT was ≤ 200 or $\geq 2,000$ ms (<3% of all trials). Statistical analyses were carried out using MATLAB 7.1 (The MathWorks) and SPSS (version 18.0).

EEG recording and analysis

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1,000, and sampled at 250 Hz. Impedances were kept below 50 k Ω and the recording was initially referenced to the vertex electrode (Cz). Signal was preprocessed using EEGlab 7.1.4 (Delorme and Makeig

Fig. 1 Behavioral procedure. One hundred and twenty trials of each delay condition were presented to participants within a session. Delay conditions 1, 2, and 3 determined whether the target disappeared 1, 2, or 3 s before the auditory cue to respond, respectively





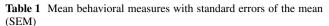
2004), running under MATLAB 7.1 (The MathWorks). Signal was bandpass filtered from 0.5 to 50 Hz and was rereferenced to a common average. Independent component analysis (ICA) was then performed to detect and remove artifacts from the data. Those components accounting for stereotyped artifacts, including eyeblinks, eye movements, and muscle movements, were identified and removed from the data. Artifactual components were determined by visual inspection of the spectral characteristics, time courses, and spatial topographies of all components. Visual inspection of the data revealed eight subjects who had a few continuously bad channels throughout the recording (mean 12 bad channels, SD = 8.9). For each subject, these channels were rejected and interpolated using splines. EEG was segmented into 1,100-ms epochs, time-locked to the auditory cue to respond (epochs extended from 100 ms prior to the tone to 1,000 ms after the tone). Trials were averaged together and baseline-corrected relative to prestimulus activity (-100 to 0 ms). On average, 117 trials of each condition per subject were retained. The maximum negative (N170) peak values between 150 and 300 ms were extracted, and mean voltages were calculated across a window extending one sample in either direction of the peak's maximum. Initially, we extracted the N170 between 100 and 300 ms in an effort to remain consistent with Cruikshank et al. (2012). However, due to individual subject variability in the peaks, mean values were more consistent with the grand average ERP figure when adopting a slightly narrower, more conservative window. It is important to note that this 150- to 300-ms window did not differentially affect the statistical outcome of our results. Peak latency was also quantified, based on the peak's maximal value. Analysis of the N170 was conducted at left and right temporal electrode clusters, comprised of seven adjacent electrodes centered around T5 and T6, respectively. Individual electrodes' peak values were averaged together for each cluster. Statistical analysis was conducted using SPSS version 18.0. Bonferroni corrections were also applied where appropriate and Greenhouse-Geisser corrections were made for violations of sphericity.

Results

Behavioral measures

Mean RT, absolute error, and MT are reported in Table 1.

Average RT, absolute error, and MT were compared between the three delays using one-way repeated-measures ANOVAs. There was a main effect of delay length on RT, which indicated a decrease in RT as delay length increased, F(1.15, 29.96) = 95.89, p < 0.01. Pairwise comparisons revealed that all delay conditions were significantly



	1 s Delay	2 s Delay	3 s Delay
Reaction time	352.0 (11.1)	311.3 (10.0)	303.8 (10.1)
Absolute error	6.5 (0.4)	7.1 (0.4)	7.6 (0.5)
Movement time	561.6 (23.5)	610.2 (24.6)	639.7 (25.1)

 $\begin{tabular}{ll} \textbf{Table 2} & Mean amplitudes and latencies (with SEMs) of the N170 \\ ERP component \end{tabular}$

	Left temporal	Right temporal
N170 amplitude (µV	7)	
1 s delay	-1.28(0.3)	-2.15(0.4)
2 s delay	-0.77 (0.2)	-1.48(0.3)
3 s delay	-0.85(0.2)	-1.57(0.4)
N170 latency (ms)		
1 s delay	236.01 (5.1)	241.26 (5.0)
2 s delay	228.46 (5.1)	230.40 (5.1)
3 s delay	221.17 (5.3)	231.54 (5.6)

different from one another and results are consistent with our initial study (Cruikshank et al. 2012). There was also a main effect of delay length on absolute error, F(1.68, 43.57) = 35.27, p < 0.01. As delay length increased, absolute error increased. All delay conditions significantly differed from one another. This result is consistent with our initial study (Cruikshank et al. 2012) and previous findings that actions requiring more perception-based information are less accurate because they rely on the recall of target features (Goodale et al. 1994). Finally, there was a main effect of delay length on MT, F(1.61, 41.78) = 18.57, p < 0.01. Pairwise comparisons revealed that MT for the 1-s delay was significantly shorter than the 2- and 3-s delays was not significantly different.

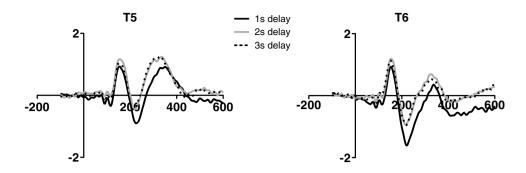
ERP measures

The mean amplitudes and latencies of the N170 component measured at left and right temporal regions are reported in Table 2. Grand average ERPs are shown in Fig. 2. We compared the amplitude of the ERP in the latency range of the N170 component across delay conditions at left and right temporal regions.

A region [2] (left temporal/right temporal) \times delay [3] (1/2/3 s) repeated-measures ANOVA revealed a main effect of delay length on N170 amplitude, F(1.49, 38.79) = 14.77, p < 0.01. Post hoc pairwise t tests revealed that N170 amplitude for the 1-s delay was significantly more negative than the 2- and 3-s delay conditions, but the N170



Fig. 2 ERP plots for T5 and T6, the central electrodes within each temporal cluster. Delay conditions 1, 2, and 3 are plotted for each electrode, with voltage (μ V) plotted on the *x*-axis and time (ms) on the *y*-axis. *Arrows* indicate the presence of an N170 component, peaking between 150 and 300 ms



amplitude between the 2- and 3-s delays was not significantly different. Taken together with the behavioral results, the N170 amplitude appeared to parallel MT, but not RT or absolute error. We wanted to determine whether any of the behavioral measures did in fact correlate with the N170 amplitude across participants, which we assessed with Spearman correlation coefficients (two-tailed) of N170 amplitude with MT, RT, and absolute error. If the N170 is relevant to planning of the reach, then a greater N170 might be associated with better reaching performance. The correlations between the averaged T5 and T6 cluster amplitude and MT and RT were not significant at any delay. However, N170 amplitude was correlated significantly with absolute error at the longest delay (3 s); when the N170 was smaller (closer to baseline) and less negative, absolute error was greater [r(26) = 0.46, p = 0.02]. The correlation was not significant at the other two delays, but in the 2-s delay condition, a trend was found [r(26) = 0.34, p = 0.08]. These results suggest that if a participant is able to maintain the N170 amplitude in the more demanding condition, their accuracy benefits.

A region [2] (left temporal/right temporal) \times delay length [3](1/2/3 s) repeated-measures ANOVA revealed a main effect of delay length on N170 latency, F(1.65, 42.82) = 7.18, p < 0.01. Pairwise comparisons revealed that the N170 peaked later in the 1-s delay condition than the 2-s and 3-s delays, which did not differ significantly. These ERP results suggest that there is a transition in the mechanisms subserving memory-guided action planning for shorter (<1 s) compared to longer delay periods.

Discussion

The aim of this study was to determine whether the same ventral stream processes are engaged and reflected by the N170 when perceptual memory is taxed beyond a few hundred milliseconds. Here, we report the presence of an N170 component during memory-guided reach initiation when 1-s, 2-s, or 3-s delays occurred between stimulus offset and the cue to respond. There were clear differences in both the

amplitude and latency of the N170 when the delay lasted only 1 s, compared to the 2-s and 3-s conditions. The N170 was more negative in amplitude and peaked later for the shorter delay period. Our results suggest that ventral mechanisms involved in movement planning differ according to the length of time a target object has been occluded.

Because the behavioral results of this study follow expected patterns, we are confident that the ERP results also reflect reliable and meaningful differences across condition. RT decreased with increasing delay period, a finding that is consistent with our earlier study, which reported a decrease in RT with target occlusion (Cruikshank et al. 2012). Also, decreasing RT as a function of increasing delay length may reflect additional levels of arousal and anticipation in the longer delay conditions (Carpenter 2004), or a lack of preparedness to respond so shortly after visual occlusion in the 1-s delay condition (Gottsdanker 1979). We also found that absolute error increased systematically with delay length. This result is consistent with earlier studies that have shown that for tasks in which the reliance on the ventral stream increases, so too does error increase (Klatzky et al. 1993; Westwood and Goodale 2003; Singhal et al. 2007; Armstrong and Singhal 2011). While these previous studies have compared visually guided (closed loop) actions to those that are memory-guided, other investigations have examined accuracy measures across closed loop, open loop, and memoryguided conditions of various delay lengths. Accuracy has been reported as being higher for closed loop compared to open loop and memory-guided tasks (Westwood et al. 2001), and many studies have revealed a reduction in reach accuracy with increasing delay period (Elliott et al. 1990; Westwood et al. 2001; Heath et al. 2004). Others have reported no diminishing of accuracy over increasing delay periods (Westwood et al. 2001; Heath and Westwood 2003; Heath et al. 2004; Heath 2005; Heath and Binsted 2007), but rather, an increase in spatial endpoint variability. This suggests that stored target information is able to provide the motor system with some substitute (albeit an unstable one) for direct target vision (Westwood et al. 2003). Our results are consistent with this notion and support the idea



that actions that engage the ventral stream rely on stored perceptual information that is less accurate than immediate visual information, inducing greater variability in arm and hand actions (Goodale and Milner 1992). In a related vein, MT toward visually precluded objects also tends to be longer (Goodale et al. 1994; Cruikshank et al. 2012) and increases with increasing task difficulty (Heath et al. 2008). We found as predicted, MT increased systematically with delay period in our task; however, they did not significantly differ between the 2- and 3-s delays. This suggests that while actions requiring more perception-based information are slower because they rely on the recall of target features (Goodale et al. 1994), there is something fundamentally different about delays extending 2 s and beyond. These behavioral effects are specific to our paradigm, as others have reported continuous decreases in MT for delays of 0-5 s (Heath and Westwood 2003). However, in that study, aiming was completed using a mouse and cursor in which the gain between the two was varied and movements toward near and far targets were compared. Therefore, differences in MT results may be attributable to differences in experimental paradigms.

The N170 ERP results follow the same pattern as the MT data, in that the 1-s delay displays significant differences compared to the 2- and 3-s delays. The N170 was less negative in amplitude and peaked earlier for the 2- and 3-s delay intervals, suggesting that the processes governing these longer memory-guided conditions, or the nature of the information supporting them, are somehow different. In this task, the properties of the target were consistent across condition; therefore, the difference in amplitude cannot be attributed to differences in the stimulus. Furthermore, the physical characteristics of the tone were also identical; thus, a difference in amplitude between conditions cannot be attributed to processes associated with the auditory tone alone. Rather, the maintenance and recall process in all conditions of our task necessitated perceptual activity in the ventral stream. However, the differential contribution of these processes according to delay length is arguably reflected by the N170 overlapping with the auditory response cue, to which the ERPs were time-locked. Our results indicate that there are differences in the neural processes underlying action planning when a delay length of 2 s or more is imposed between target disappearance and response initiation. We suggest that the N170 reflects reactivation of a stored perceptual representation in the ventral stream that is used to inform the motor plan and that this representation is susceptible to decay.

This interpretation is consistent with others' who have used behavioral and kinematic measures to investigate the time course of visual perceptual memory and the temporal durability of stored target representations supporting action (Heath et al. 2010). For example, Elliott and Madalena

(1987) reported that a brief (<2 s) visual representation is available to the motor system for online control. Similarly, Glover drew a distinction between planning and control, contending that the visual representation guiding control is transient and that it decays gradually for up to 2 s. Beyond this time, movements are executed presumably without the benefit of online control and are performed "entirely as planned", under off-line control (Glover 2004). While we cannot comment on whether the ventral stream mechanisms engaged in our task are used specifically for online control in the 1-s delay condition, we do argue that the N170 reflects reactivation of stored target information. Detailed memory representations of visual objects are known to activate areas within the LOC (Xu and Chun 2006), which are likely reactivated during recall (Nyberg et al. 2000; Wheeler et al. 2000). Because the N170 amplitude diminishes in our task, our results provide support for this theory; as delay length increases beyond 2 s, the stability of the target representation has degraded and is reflected in the smaller amplitude N170. If the stored visual representation was to be stably maintained and persisted throughout the delay, we would expect that the N170 would be comparable in amplitude across delays at the time of movement initiation. If, however, the N170 was simply a marker of increased ventral stream activity but did not index the reactivation of a previously held percept (if it only marked the demands of the memory task), we should have seen a systematic increase in amplitude with increasing delay. Finally, if there had been a sustained decay of the target representation, the N170 should have also reflected this and there should have been a systematic decrease in amplitude with increasing delay. Our results did reflect a decrease in amplitude, suggesting that decay does indeed occur. Because the difference was nonsignificant in the 2and 3-s conditions, this further supports the idea that decay has already occurred by this time and that a threshold for perceptual decay exists. While we did not include delay periods beyond 3 s, we predict that increasing time intervals would elicit N170 peaks comparable to the 2- and 3-s conditions.

Absolute error correlated with N170 amplitude in the 3-s delay condition. Thus, a larger N170 was associated with the least amount of error, but only in the condition that was most demanding of the ventral stream. This is what we would expect to find if the stored visual representation was not stably maintained or did not persist throughout the delay period. As the N170 becomes more positive, absolute error increases. Therefore, as time unfolds and the perceptual representation in the ventral stream begins to decay, the N170 amplitude decreases. We suggest that a smaller amplitude N170 reflects less reactivation, negatively affecting performance. With a more perceptually demanding task in which different, more abstract, target characteristics



require maintenance, perhaps the correlations with the other two delay intervals would emerge as significant. We did report a trend for the 2-s delay interval, and the value of the correlation increased systematically from 1- to 3-s conditions.

We must consider, however, an alternative interpretation of our findings. The mode of control and the nature of a reach may also be affected by things like visuomotor uncertainty (Heath et al. 2006). When a participant knows in advance, before the response cue, that visual information about a target will remain available, movements can be supported by online feedback mechanisms (Elliott and Allard 1985; Jakobson and Goodale 1991). However, when the predictability of visual information is unavailable (for example, a participant does not know whether he/she will be required to perform a closed loop, open loop, or memory-guided action), there is a greater reliance on ventral stream, off-line control mechanisms. In these situations, in which the participant cannot predict whether target information will disappear, movements need to be precomputed, before the response cue. In our task, participants know that every movement will be memory-guided, and the only thing that remains uncertain is the length of the delay. Due of the nature of our task, however, participants may quickly come to recognize that as time passes, the probability of an expected response increases. Consequently, an immediate anticipated response is the least predictable in the 1-s delay and the most predictable in the 3-s delay condition. After 2 s have elapsed, participants will come to learn that an imminent response will be required of them. Therefore, one could argue that unpredictable perceptual feedback could also influence the time course of the sensorimotor transformation and the mode of reaching. Just as visuomotor uncertainty results in off-line planning, perceptual uncertainty may also result in precomputing movement parameters by the ventral stream. We reported that the N170 amplitude decreased with increasing delay (although the 2- and 3-s conditions did not significantly differ from one another). While we suggest that this reflects the decay of a stored target representation, we cannot rule out the possibility that it reflects the predictability of a required response over time. The N170 could in fact be mitigated by the certainty of an upcoming response in the longer delay conditions. However, if this was the case, we might also expect to see a relationship between N170 amplitude and RT. If participants were better able to anticipate the impending response cue for the later delays, they may have been able to prepare the response slightly in advance, which would have been reflected by the N170 amplitude. Rather, we reported a correlation between N170 amplitude and absolute error, which better supports the theory of a decaying visual perceptual representation.

As reaches are planned and executed, different neural processes are engaged. To our knowledge, this is the first study to examine a known electrophysiological marker of ventral stream activity during a memory-guided task in which delay interval varies. Previous findings have revealed that the N170, overlapping with the auditory cue ERP, is a reliable marker of increased activity within the ventral stream during the planning of actions that rely more heavily on perception-based information. The current results extend this finding and suggest that the N170, while reflective of action planning, may also reflect aspects of action execution, particularly those involved in the precision of a movement. Our electrophysiological results corroborate earlier findings, which suggest that the visual representation guiding control and movement programming decays. The N170, which was previously shown to reflect the activation level of the ventral stream, appears to also reflect the accuracy of the stored visual representation when information must be held over longer periods.

References

Armstrong GA, Singhal A (2011) Neural markers of automatic and controlled attention during immediate and delayed action. Exp Brain Res 213:35–48. doi:10.1007/s00221-011-2774-0

Banko EM, Gal V, Vidnyanszky Z (2009) Flawless visual short-term memory for facial emotional expressions. J Vis 9(1):1–13. doi:10.1167/9.1.12

Batty M, Taylor MJ (2006) The development of emotional face processing during childhood. Dev Sci 9:207–220. doi:10.1111/j.1467-7687.2006.00480.x

Bentin S, Allison T, Puce A, Perez E, McCarthy G (1996) Electrophysiological studies of face perception in humans. J Cogn Neurosci 8:551–565. doi:10.1162/jocn.1996.8.6.551

Buneo CA, Jarvis MR, Batista AP, Andersen RA (2002) Direct visuomotor transformations for reaching. Nature 416:632–636. doi:10.1038/416632a

Carpenter RH (2004) Contrast, probability, and saccadic latency; evidence for independence of detection and decision. Curr Biol 14:1576–1580. doi:10.1016/j.cub.2004.08.058

Cohen NR, Cross ES, Tunik E, Grafton ST, Culham JC (2009) Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: a TMS approach. Neuropsychologia 47:1553–1562. doi:10.1016/j.neuropsychologia.2008.12.034

Cruikshank LC, Caplan JB, Singhal A (2012) Human electrophysiological reflections of the recruitment of perceptual processing during actions that engage memory. J Vis 12(29):1–13. doi:10.1167/12.6.29

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9–21. doi:10.1016/j.jneumeth.2003.10.009

Eimer M (2011) The face-sensitivity of the n170 component. Front Hum Neurosci 5:119. doi:10.3389/fnhum.2011.00119

Eimer M, Holmes A (2002) An ERP study on the time course of emotional face processing. NeuroReport 13:427–431

Elliott D, Allard F (1985) The utilization of visual feedback information during rapid pointing movements. Q J Exp Psychol A 37:407–425



- Elliott D, Madalena J (1987) The influence of premovement visual information on manual aiming. Q J Exp Psychol A 39:541–559
- Elliott D, Calvert R, Jaeger M, Jones R (1990) A visual representation and the control of manual aiming movements. J Mot Behav 22:327–346
- Elliott D, Helsen WF, Chua R (2001) A century later: Woodworth's (1899) two-component model of goal-directed aiming. Psychol Bull 127:342–357
- Fiehler K, Bannert MM, Bischoff M, Blecker C, Stark R, Vaitl D, Franz VH, Rosler F (2011) Working memory maintenance of grasp-target information in the human posterior parietal cortex. Neuroimage 54:2401–2411. doi:10.1016/j.neuroim age.2010.09.080
- Franz VH, Hesse C, Kollath S (2009) Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control. Neuropsychologia 47:1518–1531. doi:10.1016/j.neuropsychologia.2008.08.029
- Ganel T, Tanzer M, Goodale MA (2008) A double dissociation between action and perception in the context of visual illusions: opposite effects of real and illusory size. Psychol Sci 19:221–225. doi:10.1111/j.1467-9280.2008.02071.x
- Glover S (2004) Separate visual representations in the planning and control of action. Behav Brain Sci 27:3–24; discussion 24–78
- Goodale MA (1998) Vision for perception and vision for action in the primate brain. Novartis Found Symp 218:21–34; discussion 34–9
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25
- Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. Neuropsychologia 32:1159–1178
- Gottsdanker R (1979) A psychological refractory period or an unprepared period? J Exp Psychol S2:208–215
- Heath M (2005) Role of limb and target vision in the online control of memory-guided reaches. Mot Control 9:281–311
- Heath M, Binsted G (2007) Visuomotor memory for target location in near and far reaching spaces. J Mot Behav 39:169–177. doi:10.32 00/JMBR.39.3.169-178
- Heath M, Westwood DA (2003) Can a visual representation support the online control of memory-dependent reaching? Evident from a variable spatial mapping paradigm. Mot Control 7:346–361
- Heath M, Westwood DA, Binsted G (2004) The control of memory-guided reaching movements in peripersonal space. Mot Control 8:76–106
- Heath M, Rival C, Neely K (2006) Visual feedback schedules influence visuomotor resistance to the Muller-Lyer figures. Exp Brain Res 168:348–356. doi:10.1007/s00221-005-0095-x
- Heath M, Neely KA, Yakimishyn J, Binsted G (2008) Visuomotor memory is independent of conscious awareness of target features. Exp Brain Res 188:517–527. doi:10.1007/s00221-008-1385-x
- Heath M, Neely KA, Krigolson O, Binsted G (2010) Memory-guided reaching: what the visuomotor system knows and how long it knows it. In: Elliott D, Khan M (eds) Vision and goal directed movement: neurobehavioral perspectives, Human Kinetics, Champaign, IL, pp 79–95
- Hesse C, Franz VH (2009) Memory mechanisms in grasping. Neuropsychologia 47:1532–1545. doi:10.1016/j.neuropsychologia.2008.08.012
- Himmelbach M, Nau M, Zundorf I, Erb M, Perenin MT, Karnath HO (2009) Brain activation during immediate and delayed reaching in optic ataxia. Neuropsychologia 47:1508–1517. doi:10.1016/j.neuropsychologia.2009.01.033
- Hu Y, Goodale MA (2000) Grasping after a delay shifts size-scaling from absolute to relative metrics. J Cogn Neurosci 12:856–868

- Jakobson LS, Goodale MA (1991) Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res 86:199–208
- Klatzky RL, Pellegrino J, McCloskey BP, Lederman SJ (1993) Cognitive representations of functional interactions with objects. Mem Cognit 21:294–303
- Milner AD, Dijkerman HC, McIntosh RD, Rossetti Y, Pisella L (2003) Delayed reaching and grasping in patients with optic ataxia. Prog Brain Res 142:225–242. doi:10.1016/S0079-6123(03)42016-5
- Morgan HM, Klein C, Boehm SG, Shapiro KL, Linden DE (2008) Working memory load for faces modulates P300, N170, and N250r. J Cogn Neurosci 20:989–1002. doi:10.1162/j ocn.2008.20072
- Murata A, Gallese V, Kaseda M, Sakata H (1996) Parietal neurons related to memory-guided hand manipulation. J Neurophysiol 75:2180–2186
- Nyberg L, Habib R, McIntosh AR, Tulving E (2000) Reactivation of encoding-related brain activity during memory retrieval. Proc Natl Acad Sci USA 97:11120–11124
- Rossion B, Joyce CA, Cottrell GW, Tarr MJ (2003) Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. Neuroimage 20:1609–1624
- Schenk T, McIntosh RD (2010) Do we have independent visual streams for perception and action? Cogn Neurosci 1:52–62. doi:10.1080/17588920903388950
- Singhal A, Kaufman L, Valyear K, Culham J (2006) fMRI reactivation of the human lateral occipital complex during delayed actions to remembered targets. Vis Cogn 14(1):125–128
- Singhal A, Culham JC, Chinellato E, Goodale MA (2007) Dual-task interference is greater in delayed grasping than in visually guided grasping. J Vis 7(5):1–12. doi:10.1167/7.5.5
- Singhal A, Monaco S, Kaufman LD, Culham JC (2013) Human FMRI reveals that delayed action re-recruits visual perception. PLoS ONE 8:e73629. doi:10.1371/journal.pone.0073629
- Sreenivasan KK, Katz J, Jha AP (2007) Temporal characteristics of top-down modulations during working memory maintenance: an event-related potential study of the N170 component. J Cogn Neurosci 19:1836–1844. doi:10.1162/jocn.2007.19.11.1836
- Westwood DA, Goodale MA (2003) Perceptual illusion and the realtime control of action. Spat Vis 16:243–254
- Westwood DA, Dubrowski A, Carnahan H, Roy EA (2000) The effect of illusory size on force production when grasping objects. Exp Brain Res 135:535–543
- Westwood DA, Heath M, Roy EA (2001a) The accuracy of reaching movements in brief delay conditions. Can J Exp Psychol 55:304–310
- Westwood DA, McEachern T, Roy EA (2001b) Delayed grasping of a Muller-Lyer figure. Exp Brain Res 141:166–173. doi:10.1007/ s002210100865
- Westwood DA, Heath M, Roy EA (2003) No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. J Mot Behav 35:127–133. doi:10.1080/00222890309602128
- Wheeler ME, Petersen SE, Buckner RL (2000) Memory's echo: vivid remembering reactivates sensory-specific cortex. Proc Natl Acad Sci USA 97:11125–11129
- Wronka E, Walentowska W (2011) Attention modulates emotional expression processing. Psychophysiology 48:1047–1056. doi:10.1111/j.1469-8986.2011.01180.x
- Xu Y, Chun MM (2006) Dissociable neural mechanisms supporting visual short-term memory for objects. Nature 440:91–95. doi:10.1038/nature04262

