



Visual processing at goal and effector locations is dynamically enhanced during motor preparation[☆]



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ABSTRACT

Previous theoretical and experimental works has shown that preparing to act causes enhanced perceptual processing at movement-relevant locations. Up until now, this has focused almost exclusively on the goal of an action, neglecting the role of the effector. We addressed this by measuring changes in visual processing across time during motor preparation at both goal and effector locations.

We compared event related potentials (ERPs) elicited by task-irrelevant visual probe stimuli at both goal and effector locations during motor preparation. Participants were instructed to place their hands on two starting positions (effector locations) and an auditory tone instructed them to immediately move to one of two target buttons (goal locations). Probe stimuli were presented in the interval between the offset of the cue and the execution of the movement at either a goal or an effector location. Probes were presented randomly at either 100 ms, 200 ms or 300 ms after the auditory cue.

Analysis of the visual N1 ERP showed enhanced visual processing at moving vs. not-moving goal locations across all three SOAs. At effector locations, enhanced processing for the moving vs. not-moving effector was only observed during the middle (200 ms) SOA.

These results demonstrate, for the first time, simultaneous perceptual enhancement of goal and effector locations during motor preparation. We interpret these results as reflecting a temporally and spatially specific dynamic attentional map of the environment that adapts to maximise efficiency of movement by selectively weighting processing of multiple functional components of action in parallel.

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Introduction

To interact effectively with the physical environment requires us to plan action as efficiently as possible. The importance of accurate and effective action is reflected in the fact that motor preparation has effects on cognitive processes other than the purely motoric. One such process that has been well studied is visual perception, which is enhanced in a spatially selective manner by an intention to perform a goal directed action. This enhancement can be measured using behavioural, electro-physiological or other neuroimaging measures of visual processing, and allows us to make inferences about the underlying stages of motor processing that cause it, for example by comparing visual processing at locations involved in action with those that are not.

Whilst this approach has consistently demonstrated perceptual enhancement at the location of the goal of action, the influence of motor

preparation on visual perception near the effector has been comparatively neglected. This has led to a situation whereby very little work has systematically addressed the influence of the effector location in action planning in human participants (though see Eimer et al., 2005; Forster and Eimer, 2007; Juravle and Deubel, 2009; Juravle et al., 2011 for somatosensory processing on the hand), which in turn has led to potentially simplistic modelling of the effects of movement preparation on sensory processing with an undue focus on goal locations.

The Premotor Theory of Attention (Rizzolatti et al., 1987, 1994) and the Visual Attention Model (Schneider, 1995) provide frameworks for understanding the perceptual consequences of action preparation. The Premotor Theory predicts that space is represented in the brain by effector-specific “spatial pragmatic maps” in the parietal cortex (Rizzolatti et al., 1994, p. 231), responsible both for the perception of space and for the planning of action. An intention to act upon a particular area of space causes a motor program to be set up within an effector-specific map, and until it is executed the activity of neural populations that code for the perception of that area of space is facilitated. This facilitation then exerts a top down effect on visual processing. Whilst the theory maintains that spatial attention arises from facilitation associated with the preparation of goal-directed action, it does not explicitly limit the scope of this facilitation to goal locations, and the principles it

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establishes could equally well be expected to apply to any action-relevant locations in space, such as those of the effector.

The majority of experimental tasks used to study the perceptual consequences of an intention to act were developed to investigate the programming of saccades. The effects on perception of preparing to make a saccade are remarkably similar to those seen in tasks that manipulate covert spatial attention; discrimination and detection of visual targets at the goal of a saccade are facilitated (Hoffman and Subramaniam, 1995; Posner, 1980; Rizzolatti et al., 1987; Schneider and Deubel, 1995; Shepherd et al., 1986). Consistent with these behavioural observations, electrophysiological work has shown enhanced activity in extrastriate visual areas when stimuli were presented at goal locations during saccade preparation (Eimer et al., 2006), effects highly reminiscent of those observed in tasks involving cued spatial attention (e.g. Mangun and Buck, 1998). Similar approaches have more recently been applied to manual movements. Enhanced processing at goal locations has been demonstrated during the preparation of pointing (Baldauf and Deubel, 2008b; Deubel et al., 1998), reaching (Baldauf and Deubel, 2008a; Baldauf et al., 2006) and grasping (Gilster et al., 2012; Schiegg et al., 2003) movements.

Further, lateralisation of event-related potentials (ERP) elicited in response to spatial cues that are thought to represent the operation of a frontoparietal attentional control network (ADAN, LDAP, Eimer and Van Velzen, 2002; Hopf and Mangun, 2000; Nobre et al., 2000) have been observed when shifting spatial attention (Eimer and Van Velzen, 2002; Van Velzen et al., 2002) but also when preparing saccades (Eimer et al., 2007; Gherri and Eimer, 2008; Wauschkuhn et al., 1998; Van der Lubbe et al., 2006) and manual movements (Gherri and Eimer, 2010; Gherri et al., 2007; Mathews et al., 2006; Praamstra et al., 2005; Wascher and Verleger, 1997). These findings suggest shared sensorimotor control mechanisms involved in attentional orienting and in programming motor responses and are consistent with fMRI evidence showing a considerable overlap in activated brain regions during both types of task (Astafiev et al., 2003; Corbetta et al., 1998; Perry and Zeki, 2000; De Haan et al., 2008). More spatially fine-grained methods of investigating this overlap, however, have shown segregation between the planning of saccades and covert shifts of attention in areas of the Posterior Parietal Cortex (PPC). Whilst the Intraparietal Sulcus (IPS) is activated in attention and saccade preparation (Colby et al., 1996; Gaymard et al., 1998) it does not reliably predict the onset of a saccade (Bisley and Goldberg, 2003). Smith and Schenk (2012) suggest that the IPS represents a “priority map” (p. 1106) that codes behaviourally relevant locations. Whilst saccade targets and the locus of covert attention may indeed be behaviourally relevant – and so coded for by the IPS – this does not mean that IPS involvement is obligatory for both motor preparation and saccade programming, but may operate more broadly. This is an intriguing suggestion in the context of goal and effector locations since whilst enhanced processing at the location of an effector is at odds with the goal-centric predictions of the Premotor Theory, effectors are clearly behaviourally relevant during the preparation of a reaching movement.

Studies that have used measures of visual perception during goal directed action show that task instructions that emphasise either the goal or the effector can alter the balance of processing priorities between the two (Gherri et al., 2009; Van Velzen et al., 2006). Whilst this work shows that perceptual enhancement at the effector location can happen in principle, their pattern of results suggests that this effect may be limited to either goals or effectors, dependent upon top down factors such as task instructions. This interpretation is inconsistent with findings that suggest that the coupling between action and perception at the goal location is obligatory (Deubel and Schneider, 1996; Hoffman and Subramaniam, 1995; Schiegg et al., 2003; Schneider and Deubel, 1995, 2002, though see also Belopolsky and Theeuwes, 2009; Deubel, 2008; Hunt and Kingstone, 2003, for arguments to the contrary). A possible explanation may be found in terms of the time course of motor preparation: if the temporal sequence of goal and effector

processing differs (perhaps due to differing underlying mechanisms, e.g. Cisek and Kalaska, 2010) then the discrepancies in terms of enhancement at goal and effector locations in previous studies may be due to perceptual processing being measured at a point in time when *either* goal or effector processing is occurring, thus ‘missing’ the perceptual enhancement of the other component of action.

Making use of the excellent temporal resolution of event-related potentials (ERPs), electrophysiological studies into effects of movement preparation on visual processing typically use a delayed response paradigm. In this approach the participant receives instruction from two separate symbolic cues, the first (S1) instructing them which location to prepare a movement toward; and the second (S2) instructing them to actually execute it (or in some cases to withhold execution). Task irrelevant probe stimuli are presented in the delay between the two. The advantage of this method is that it allows temporal separation of movement preparation and the concomitant effect on sensory processing, but a disadvantage is that the delay causes the participant to be in a somewhat artificial state of anticipation, having planned an action but waiting to execute it. In contrast, most behavioural studies have used immediate response paradigms in which one cue instructs the participants where to move and also serves as a signal to execute the movement. However these designs require participants to make a response to probe stimuli, thus introducing a secondary task and reducing ecological validity.

In the present study we made use of the strengths of both approaches to investigate the interaction between action planning and visual processing at both the goal and the effector location during movement preparation. To achieve this we used the amplitude of the N1 component of the visual ERP as an index of extrastriate cortical activity in response to task-irrelevant visual probe stimuli presented at effector and goal locations. Unlike previous ERP studies that used a delayed-response paradigm, our participants executed a reaching movement as soon as a cue instructed them where to move, allowing us to measure the neural correlates of action planning on perception in a temporally sensitive manner. By assessing perceptual processing at multiple time points we were able to investigate whether the effects on visual processing at goals and effectors are specific to each location, and whether such processing can occur in parallel.

Method

Participants

A sample of 14 participants (12 females) took part in the experiment after giving informed consent. Some were paid in cash, and some received course credit as payment for participation. Participants ranged in age from 19 to 29 (mean age was 23.4 years), all were right handed by self report, had normal or corrected-to-normal vision and none had been diagnosed with any movement disorders. One participant was excluded from ERP analyses due to excessive eye movements, leaving a total of 13 participants. The study was approved by Goldsmiths' ethics committee and informed consent was obtained from all participants.

Apparatus

The experiment was conducted on a movement console which consisted of a gently sloped surface with a separate haptically-defined starting position for the left and right hand nearest to the participant, and separate goal buttons for the left and right hand, measuring 4 cm in diameter, located directly in front of the starting position, at a distance of 23 cm from the starting position. Starting positions and goal buttons were positioned at 18 cm from the body midline on either side.

A one-way mirror was positioned above the console, between it and the participant, above whom was a 21" CRT computer monitor with the screen facing down. The mirror was adjusted such that when the display from the monitor was reflected on the glass, it appeared to originate

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