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Spatial primes produce dissociated inhibitory effects on saccadic latencies and trajectories

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ABSTRACT

In masked priming, a briefly presented prime can facilitate or inhibit responses to a subsequent target. In most instances, targets with an associated response that is congruent with the prime direction speed up reaction times to the target (a *positive compatibility effect*; PCE). However, under certain circumstances, slower responses for compatible primes are obtained (a *negative compatibility effect*; NCE). NCEs can be found when a long pre-target delay is used. During the delay, inhibition is assumed to take place, and therefore an effect on saccade trajectories may also be expected. In a previous study, we found the effects of inhibition on response times and trajectories to be dissociated, but this experiment varied the timing of several aspects of the stimulus sequence and it is therefore unclear what caused the dissociation. In the present study, we varied only one aspect of the timing, but replicated the dissociation. By varying just the pre-target delay, we found a PCE for a short delay, and an NCE for a long delay, but saccade trajectories deviated away from prime directions in both conditions. This suggests dissociated inhibitory effects of primes on response times and saccade trajectories.

1. Introduction

Visual cues such as arrows presented at fixation have been shown to influence manual and saccadic responses to subsequent target stimuli by producing faster reaction times when the two are at corresponding spatial locations (Kuhn & Benson, 2007; Posner, 1980). These cues can affect responses to the target even when presented for a very brief time, rendering the cue almost invisible. This phenomenon is known as masked priming, in which the cue is referred to as a 'prime'. In most instances, primes with an associated response compatible with the target direction produce faster response times to the target. However, under certain conditions, congruent primes have been shown to slow responses to the target (Eimer & Schlaghecken, 1998). This 'negative compatibility effect' (NCE) has been replicated numerous times (Eimer, 1999; Klapp & Hinkley, 2002; Schlaghecken & Eimer, 2002) and appears to be predominant under conditions of low prime visibility, but can also appear in situations where prime detection is above chance levels (Schlaghecken et al., 2007; Sumner et al., 2006).

In typical priming, the prime firstly automatically activates a congruent response. When a congruent target is then presented, it benefits from the response preparation of the prime, resulting in faster response times for congruent prime–target combinations. For incongruent combinations, the automatic activity for the prime needs to be inhibited, before the correct target response is initiated, which slows responses. This pattern of response times is the positive compatibility effect (PCE). Evidence for this can be seen in EEG measures such as those associated with response preparation (e.g. lateralised readiness potential), which show an early response to the prime, followed by a later, stronger response to the target (Kopp et al., 1996).

The opposite response time pattern found in NCEs can be explained with one additional assumption – that the automatic activity following the prime is suppressed over time to a level below baseline. This assumption is made by the motor inhibition hypothesis (Eimer & Schlaghecken, 1998; Sumner, 2007). When a prime-congruent target is presented during this suppression of prime-related activity, it will lead to slower responses than an incongruent, and even a neutral prime. So, with longer intervals between the prime and the target, where the activity associated with the prime is suppressed, we expect to find an NCE. This below-baseline suppression is supported by the finding that, when given a free choice of whether to execute left or right responses, participants generally choose the response opposite to the inhibited prime despite being unaware of such behaviour (Klapp & Hinkley, 2002).

Positive compatibility effects (PCEs) are generally found when the overall temporal inter-stimulus interval (ISI) between prime offset and target onset is 0–60 ms (Sumner, 2007). It is at a longer

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ISI of 100–200 ms that NCEs begin to appear with performance benefits for incongruent trials. Primes that take a different form to traditional arrows, such as circles with rightward or leftward gaps, are capable of producing NCEs, but tend to begin functioning in this way at longer exposure times, arguably due to eliciting weaker motor activation in the first place (Schlaghecken et al., 2007). Although differing in levels of effect, NCEs are robustly found across varying conditions, and much support exists for the motor inhibition model (Schlaghecken et al., 2007; Sumner, 2007; Vainio, 2011). The inhibitory processes that produce NCEs may be generated at two different levels – they could be self-generated by the motor system itself, or could be reactions to stimuli within the task (Boy, Clarke, & Sumner, 2008; Jaśkowski, 2008).

Some models attempt to explain NCEs without invoking inhibition. According to the object-updating account (Lleras & Enns, 2004), the structure presented after the prime, but before the target (the mask) is essential. Only masks with a task-relevant structure in terms of target identity can produce an NCE. Task relevant features present in the mask are assumed to update the motor system following prime-related automatic activation, producing preparatory activity for an alternative response, resulting in faster responses to incongruent targets. The object-updating account therefore suggests that reaction time benefits for incongruent trials in NCEs may not be caused by inhibition of the prime response, but instead by positive priming for the alternative response by a task-relevant mask. A number of experiments have shown that sequences using task-irrelevant masks produce PCEs rather than NCEs despite successful reduction of prime visibility. This lack of an influence of masks that do not have target-related features is attributed to the masks not updating the motor system with preparation for the alternative response (Lleras & Enns, 2004). In this context, it is important to note that the task-relevance of a mask may not only depend on geometric and structural similarities between target and mask (Jaśkowski & Przekoracka-Krawczyk, 2005; Lleras & Enns, 2006), but also on spatial and temporal similarities (Lleras & Enns, 2006).

These accounts have been useful in revealing alternative conditions under which NCEs can be obtained, but motor inhibition appears to be the main source of the NCE when task-irrelevant masks (e.g. random line masks) are used (Sumner, 2008). The inhibitory processes underlying the NCE are still not fully understood however and further evidence is required. One approach to improving understanding of the inhibitory processes involved is to examine other behavioural responses associated with motor inhibition, and compare the resulting effects. One such phenomenon is that of curved saccade trajectories. Saccade trajectories have been shown to provide a sensitive measure of response inhibition (Doyle & Walker, 2001; McSorley, Haggard, & Walker, 2006; Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel, Meeter, & Theeuwes, 2007; Van der Stigchel & Theeuwes, 2005). Trajectories of saccades are often found to deviate away from a previously attended location, or from the location of a peripheral distractor onset. Saccade trajectories have also been shown to deviate away from attended locations during inhibition of return (IOR), where slower reaction times are recorded when responses are made to cued rather than uncued peripheral locations (Godijn & Theeuwes, 2004; Theeuwes & Van der Stigchel, 2009). Saccade deviations are attributed to inhibition in the spatial maps that encode potential saccade targets, such as that thought to be formed by neurons in the superior colliculus (SC) (Aizawa & Wurtz, 1998; McPeek, 2006; McPeek, Han, & Keller, 2003). Evidence for the role of inhibition in these maps was found by directly recording from cells in the SC – positive curvature was found following microstimulation of SC cells, with increased activation for distractor locations correlating with increased curvature (McPeek, 2006; McPeek, Han, & Keller, 2003). The inhibition of the distractor-related activity may depend on inhibitory projections from the substantia nigra rather than on top-down signals from cortical oculomotor centres (White, Theeuwes, & Munoz, 2011, 2012). Similar to the motor inhibition account of the NCE, the modulation of trajectory deviation has been found to depend on the time course, with deviation towards occurring for short latency responses and deviation away occurring at longer latencies (McSorley, Haggard, & Walker, 2006).

Because of the strong similarities between the assumed underlying mechanisms of the NCE and saccade trajectory deviations, the two phenomena have been studied in conjunction, by adopting a paradigm in which saccadic response times and trajectories were measured under highly similar conditions (Hermens, Sumner, & Walker, 2010). The expectation in this study was that saccades would deviate in the direction of primes during PCE reactions, but away from the direction of primes with NCEs that allow inhibition to be applied to that location in the motor map. In contrast to this prediction, strong trajectory deviations away from the prime directions were found during PCE reactions with non-significant deviation under NCE conditions (Hermens, Sumner, & Walker, 2010). This suggested a general dissociation between the activation and inhibition processes that lead to the PCE/NCE effects, and the inhibitory spatial processes behind saccade curvature, but it was unclear what could have led to this dissociation, because the PCE and NCE effects in the study were generated by varying several aspects of the stimulus timing. For this reason, a number of possible factors were identified, including the durations of the prime, the mask and the delays, which may all have contributed to the dissociation of the two effects (NCE and saccade trajectories).

To establish the source of the dissociation between saccadic response times and saccade trajectories, the present study keeps all the stimulus timings constant across two conditions (short-ISI and long-ISI), and only manipulates the interval between the mask and target designed to vary the overall-ISI between prime offset and target onset. This interval between mask and target will be referred to as the 'pre-target-delay' to distinguish it from the overall-ISI. As in Hermens, Sumner, and Walker (2010), saccadic response times and curvature are measured, by the inclusion of prime-and-target congruent and incongruent trials as well as oblique 'probe' trials aimed to measure trajectory curvature.

By keeping all stimulus factors constant except for the pre-target-delay, we can directly test the influence of the overall-ISI as a critical factor in the PCE and NCE. The overall-ISI has previously been shown to be an important factor in response times (e.g. Boy & Sumner, 2010), but its influence on saccade trajectories is unclear. It is predicted that short-ISI conditions will produce PCEs while long-ISI conditions will show NCEs in saccade latency. A dissociation between response time effects and curvature effects is expected only if different underlying activation/inhibition processes cause the two effects. After pilot testing,[1] we found a stimulus combination in which a variation of just the pre-target-delay led to a PCE in one condition and an NCE in another condition. With this combination, we tested a total of 31 participants to examine whether a similar pattern on saccade trajectories could be found.

2. Methods

2.1. Participants

Thirty-one participants (12 male), aged between 19–40 years took part in the experiment. These included students at Royal

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[1] 12 participants were tested in an initial pilot with 100 ms masks and a 50 ms pre-target delay for the long-ISI condition (no delay for short-ISI). Both short and long-ISI conditions produced NCE effects, suggesting that the overall-ISI was too long. For the experiment in the current paper, we reduced the mask duration to 40 ms in order to get PCE and NCE effects in short and long-ISI conditions respectively.