



Inhibition of masked primes as revealed by saccade curvature

Frouke Hermens^a, Petroc Sumner^b, Robin Walker^{a,*}

^a Department of Psychology, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK

^b School of Psychology, Cardiff University, Cardiff CF10 3AT, UK

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ABSTRACT

In masked priming, responses are often speeded when primes are similar to targets ('positive compatibility effect'). However, sometimes similarity of prime and target impairs responses ('negative compatibility effect'). A similar distinction has been found for the curvature of saccade trajectories. Here, we test whether the same inhibition processes are involved in the two phenomena, by directly comparing response times and saccade curvature within the same masked priming paradigm. Interestingly, we found a dissociation between the directions of masked priming and saccade curvature, which could indicate that multiple types of inhibition are involved in the suppression of unwanted responses.

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1. Introduction

In everyday life, we are confronted with a stream of visual inputs that needs to be processed to extract information that is relevant for our on-going behavior while avoiding responses to irrelevant stimuli. We here investigate the processes that underlie such response selection by comparing two different measures: response times and the curvature of saccade trajectories, both measured in the same masked priming paradigm. Our results suggest that multiple mechanisms might be at work in the selection of an appropriate response to incoming information.

While parts of the processes underlying response inhibition are under voluntary control, a large section may occur automatically. One paradigm often used to investigate such automatic activation and inhibition of responses to incoming stimuli is masked priming. In masked priming, a prime preceding the target influences response times and error rates to the target (e.g. Leuthold & Kopp, 1998; Neumann & Klotz, 1994). Typically, the prime is presented for a very brief duration, and it is masked, either by a separate mask, or by the target. This masking has the consequence that if participants are asked to report the identity of the prime, they are often close to chance level. For this reason, the influences exerted by masked primes are thought to reflect automatic processing, possibly through direct perceptuo-motor links, providing a direct pathway from sensory to motor processing (e.g. Klotz & Neumann, 1999).

The most common effect a prime has on the response to the target is that response times are faster and errors occur less often

when the prime is identical or similar to the target, in comparison to when the prime is unrelated to the target or has features associated with the opposite response. However, under certain conditions, for example, when the time between the presentation of the prime and the target is long, the pattern reverses, and response times are slower when the prime and the target are similar or identical (for reviews see Eimer & Schlaghecken, 2003; Sumner, 2007). The reduction in response times with compatible primes is often referred to as straight priming (Jaśkowski & Verleger, 2007) or the positive compatibility effect (PCE), and the increase in response times with compatible primes is called inverse priming or the negative compatibility effect (NCE). Negative compatibility effects are found only if the time between the presentation of the prime and the presentation of the target is sufficiently long. Keeping the stimuli and task constant, varying the prime-to-target interstimulus interval (ISI), a shift from a positive to a negative compatibility effect is found at intervals around 80 ms (Fig. 1 of Bowman, Schlaghecken, & Eimer, 2006). Additionally, NCEs are more often found when the prime is just below the threshold for conscious detection (e.g. Eimer & Schlaghecken, 2002), although they can also be found for visible primes (Klapp & Hinkley, 2002; Sumner, Tsai, Yu, & Nachev, 2006).

The cause of the negative compatibility effect is highly debated. One explanation, known as the self-inhibition hypothesis, assumes that motor program activated by the prime is automatically suppressed (e.g. Bowman et al., 2006; Eimer & Schlaghecken, 1998; Klapp & Hinkley, 2002; Schlaghecken, Bowman, & Eimer, 2006; Schlaghecken & Eimer, 2006). If the target is presented at the time the prime response is still active, a PCE occurs. If the target is presented later, once the prime response has been suppressed, then a

* Corresponding author. Fax: +44 1784434347.

E-mail address: robin.walker@rhul.ac.uk (R. Walker).

NCE is observed. Such an explanation is supported by EEG recordings, showing a triphasic pattern of preparatory motor activation following the sequence of prime, mask and target (Eimer, 1999; Eimer & Schlaghecken, 1998) (however, see Verleger, Jaśkowski, Aydemir, Van der Lubbe, & Groen, 2004 for an alternative explanation), in which the first phase corresponds to prime activation, the second one with prime suppression and the third one with target activation (Eimer & Schlaghecken, 2003; Praamstra & Seiss, 2005). An alternative explanation was suggested by Verleger and colleagues (2004) (see also, Lleras & Enns, 2004, 2005, 2006) and is known as the active mask, or object-updating hypothesis. This theory proposed that, rather than self-inhibition, interactions between the prime and the mask occur that cause the priming to reverse. Such interactions only occur if elements of the prime are also present in the mask, which means that it cannot account for all NCEs (Jaśkowski, 2009; Schlaghecken & Eimer, 2006; Sumner & Brandwood, 2008). Finally, there is the ‘mask-triggered inhibition’ hypothesis (Boy, Clarke, & Sumner, 2008; Jaśkowski & Verleger, 2007; Jaśkowski, 2008; Jaśkowski & Przekoracka-Krawczyk, 2005) which assumes that inhibition of the prime is caused by another stimulus that requires attention, being the mask, or the target. However, in all three theories, a response to the prime in a typical prime–mask–target sequence is initially activated followed by a relative suppression of this prime related activity.

Similarly, studies of saccadic eye movements have shown that the trajectory of an eye movement can be modulated under conditions in which one of the responses has to be inhibited (Doyle & Walker, 2001; McSorley, Haggard, & Walker, 2004, 2005, 2006, 2009; Mulckhuysse, Van der Stigchel, & Theeuwes, 2009; Van der Stigchel, Meeter, & Theeuwes, 2007a, Van der Stigchel, Meeter, & Theeuwes, 2007b; Van der Stigchel & Theeuwes, 2005, 2006, 2008; Van der Stigchel, Mulckhuysse, & Theeuwes, 2009; Theeuwes & Van der Stigchel, 2009; Van Zoest, Van der Stigchel, & Barton, 2008; Walker, McSorley, & Haggard, 2006). These studies have shown that saccade trajectories deviate away from an attended location (Nummenmaa & Hietanen, 2006; Sheliga, Riggio, & Rizzolatti, 1994; Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Van der Stigchel et al., 2007b) and away from the location of an eccentric distractor (Doyle & Walker, 2001; McSorley et al., 2004, McSorley, Haggard, & Walker, 2005, 2006, 2009; Van Zoest et al., 2008; Walker et al., 2006). However, in some situations trajectories tend to deviate towards the distractor (McPeck, Han, & Keller, 2003; McPeck & Keller, 2001; Walker et al., 2006). Studies of the activity of cells in the monkey superior colliculus (SC) and frontal eye fields (FEFs) have demonstrated that multiple sites in these structure are active prior to curved saccades (McPeck & Keller, 2001; McPeck et al., 2003; Port & Wurtz, 2003). Specifically, distractor related activity above baseline resulted in a curvature towards the distractor, whereas activity below baseline cause deviation away from the distractor location (McPeck et al., 2003). Moreover, inhibiting activity by injecting the GABA agonist muscimol caused saccades to curve away from the inhibited site (Aizawa & Wurtz, 1998). The prevalent view is that saccade curvature arises when multiple saccade goals are activated in the brain areas in the process of saccade target selection, and that curvature away from a site is found when activity is suppressed below baseline (McSorley, Haggard, & Walker, 2006).

The modulation of saccade trajectory deviation is often regarded as a proxy to the distribution of activation and inhibition in the neural structures involved in encoding potential saccade targets prior to saccade onset (McPeck, 2006). In the present study saccade trajectory deviation is used as an alternative way of probing the automatic response selection processes involved in masked priming. How this might work, is illustrated in Fig. 1, in which a hypothesized map of saccade motor activity is shown, with the amount of activity shown along the vertical dimension for different

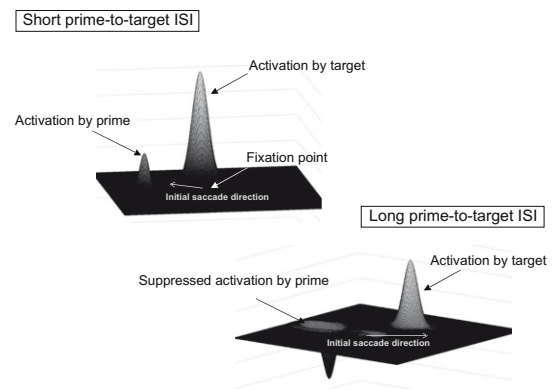


Fig. 1. Illustration of the hypothesized activity in the saccade motor map (along the vertical dimension) for different positions in space (horizontal plane) for a short prime to target interval (top) and a long interval (bottom). The gray arrow indicates the initial direction of the saccade, which follows the direction of the mean activation in the map.

positions in space (shown in the horizontal plane). If the interval between the presentation of the prime and the mask is short (top plot), activation in the map corresponding to the prime location has not yet been suppressed and the mean vector of activation (e.g. Lee, Rohrer, & Sparks, 1988) falls in between the peaks of activation representing the prime and the target location. As it is commonly assumed that saccade direction is determined by the mean vector of activation, the initial direction of the saccade will be in between the prime and the target. This initial direction error is corrected such that the eye lands on the target, with the consequence that the overall trajectory of the saccade curves towards the direction of the prime. However, if the target is presented after a longer interval (bottom plot), the activity in the map corresponding to the prime has been suppressed below baseline, and the resulting mean vector will curve the saccade away from the prime. Note that this initial activation in the direction of the prime followed by an inhibition below baseline corresponds to the first two phases observed in the EEG data (Eimer, 1999; Eimer & Schlaghecken, 1998; Verleger et al., 2004). In this respect, measuring saccade curvature could provide a measure of oculomotor preparation, just like the phases of the EEG response are thought to reflect manual response preparation.

Alternatively, saccade curvature effects and reaction time priming effects might be dissociated. Such dissociation could arise if the inhibition involved in the saccadic NCE and that involved in saccade curvature takes place at different stages of saccade programming. In ‘inhibition of return’, a phenomenon that could involve similar mechanisms as the NCE in masked priming, evidence for such dissociation was obtained (Godijn & Theeuwes, 2004; Theeuwes & Van der Stigchel, 2009). Inhibition of return occurs when a response is required to a previously attended stimulus. Typically, an irrelevant stimulus is presented in the periphery, or an item in the periphery is cued with a central cue, both of which participants are asked to ignore. After a delay, the target is presented either at the location of the irrelevant stimulus or at a different location. If the delay is short, responses to the same location are faster. However, for longer delays, slower response times are found when the target is presented at the same position as the ignored stimulus. IOR and masked priming may involve similar processes, because they both show a reversal of congruency effects at longer cue or prime to target intervals.

Godijn and Theeuwes (2004) investigated the relation between inhibition of return and saccade curvature by comparing the time-course at which they take place. In addition, the effects of the salience of the cue and the type of cue (exogenous versus endogenous) were studied. Whereas cue salience and cue type had

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