Visual attention amplifies response priming of pointing movements to color targets

(Ms. P451)

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Manuscript information:
7 figures, 54 references
abstract: 142 words; main text: 6,642 words

Abstract

We studied the influence of spatial visual attention on the time-course of primed pointing movements. We measured pointing responses to color targets preceded by color stimuli priming either the same or opposite response as the targets. Effects of visual attention at the prime/target locations were studied by giving endogenous attentional cues whose processing was a precondition for performing the task, or exogenous cues, varying both the cue-prime and the prime-target interval. Pointing trajectories revealed large priming effects such that pointing responses were first controlled by prime signals and then captured in mid-flight by target signals. Priming effects were strongly amplified when the relevant prime locations were visually attended at optimal cue-prime SOAs, with attention modulating the entire time-course of primed pointing movements. We propose that visual attention amplifies the earliest waves of visuomotor feedforward information elicited in turn by primes and targets.

Keywords:

Priming; Response Priming; Visual Attention; Pointing Movements

Introduction

Visual attention and feedforward processing. The modulating effects of visual attention on cortical stimulus processing have been studied extensively. There are several mechanisms how visual selective attention modulates the responses of individual cells (Kastner & Ungerleider, 2000; Yantis & Serences, 2003), one of them being the modulation of processing sensitivity (e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Corbetta et al., 1991). Treue and Martínez Trujillo (1999) showed that attention directed to a particular stimulus feature enhanced responses of cells in cortical area MT selective for that stimulus feature. The enhancement was multiplicative, affecting the entire tuning curve. Similar results have been reported for area V4 (McAdams & Maunsell, 1999; Reynolds, Pasternak, & Desimone, 2000), indicating that the effects of attentional enhancement are similar to an increase in effective stimulus contrast (e.g., Boynton, 2005; Reynolds & Chelazzi, 2004).

Recently, theoreticians have started to distinguish between two fundamentally different types of visual processing: a rapid feedforward process where visual activation proceeds in bottom-up direction through the visual system (Bullier, 2001; Thorpe, Fize, & Marlot, 1996; VanRullen & Koch, 2003; VanRullen & Thorpe, 2002), and the slower, recurrent interactions developing in the immediate wake of this "fast feedforward sweep" (Lamme & Roelfsema, 2000; Lamme, 2002, 2006).[1] In the context of such models, visual attention is typically conceived as a top-down influence of areas late in the processing stream on earlier areas via feedback connections, and is thereby linked to reentrant activity developing during processing of a stimulus, as well as the development of visual awareness (DiLollo, Enns, & Rensink, 2000; Lamme, 2002, 2006; Lamme & Roelfsema, 2000; Lamme, Zipser, & Spekreijse, 2002; Tong, 2003).

However, reentrant attentional processes modulating the response properties of early visual areas could also play a part in the feedforward component of visual processing: If attentional selection is complete ***before*** the critical stimuli are presented, attention should be able to aid in all phases of subsequent stimulus processing (Desimone & Duncan, 1995). In this paper, we are interested in such effects of attention on the bottom-up flow of information, examining attentional effects in a ***response priming*** paradigm. We investigated the time-course of primed pointing movements because this variant of response priming has been strongly linked to the initial feedforward component of visuomotor processing.

Response priming and rapid-chase theory. In the standard response priming paradigm (Klotz & Neumann, 1999; Neumann & Klotz, 1994), participants have to perform a speeded response to a target stimulus that is preceded by a prime stimulus triggering either the same response as the target ***(consistent prime)*** or the opposite response ***(inconsistent prime).***

Consistent primes speed responses while inconsistent primes prolong them, and this priming effect increases with stimulus-onset asynchrony (SOA) between prime and target onset, up to SOAs of about 100 ms (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). Inconsistent primes can actually elicit the wrong response, particularly at long SOAs, while response errors rarely occur with consistent primes. Strikingly, response priming effects are independent of visual awareness of the prime: Their increase with SOA is invariant no matter whether the prime can be identified perfectly or not at all, and no matter whether prime identification performance increases or decreases with SOA (Mattler, 2003; Schmidt & Vorberg, 2006; Vorberg et al., 2003). These dissociations suggest that priming effects reflect a fast-acting impact of the prime on motor responses which is independent of subsequent masking processes, whereas visual awareness of the prime develops later and integrates information from both primes and masks (DiLollo et al., 2000; Lamme et al., 2002).

Results from psychophysiological and imaging studies have indeed shown that primes directly initiate the specific motor responses assigned to them, leading to elicitation of lateralized readiness potentials (*LRPs,* Eimer & Schlaghecken, 1998, 2002, 2003; Leuthold & Kopp, 1998; Vath & Schmidt, 2007; Verleger, Jaśkowski, Aydemir, van der Lubbe, & Groen, 2004) and lateralized metabolic activity in motor areas (Dehaene et al., 1998). These effects can also be traced in overt pointing responses. In a study by Schmidt, Niehaus, and Nagel (2006; Schmidt, 2002), one red and one green target were presented simultaneously in diagonally opposite quadrants of a display, preceded by one red and one green prime at the same two locations. Primes could either have the same colors as the targets (consistent primes), or prime colors could be switched with respect to target colors (inconsistent primes). Speeded pointing responses toward the target of appointed color were strongly affected by the primes: The onset of the pointing movements was time-locked to primes rather than targets, and in many trials the initial response was actually in the direction of the primes, even if this movement direction turned out to be misleading and the movement had to be reversed in mid-flight. Importantly, the early time-course of the pointing trajectories was invariant across different target types and prime-target SOAs. This crucial finding suggests that pointing responses were initially independent of all target characteristics, driven solely by the prime signal.

Schmidt et al. (2006; Vath & Schmidt, 2007; see Vorberg et al., 2003, for a mathematical model) proposed a ***rapid chase theory*** of response priming that links visuomotor priming to feedforward processing. This framework assumes that prime and target signals are transmitted sequentially by early feedforward waves of visuomotor processing (Bullier, 2001; Lamme & Roelfsema, 2000; Thorpe et al., 1996; VanRullen & Thorpe, 2002) elicited in turn by primes and targets. Prime and target signals are able to directly initiate the motor responses assigned to them, with no need for conscious mediation (***direct parameter specification,*** Neumann, 1990; Neumann & Klotz, 1994; cf. Kunde, Kiesel, & Hoffmann, 2003). The prime signal reaches executive motor areas first, initiating a response and continuing to drive the response on its own. After a delay about the size of the prime-target SOA, the target signal arrives and takes over response control from the prime signal. Priming effects, as well as error rates in inconsistent trials, increase with prime-target SOA because the prime has more time to drive the response on its own when the target is further delayed. Response priming may occur overtly, with noticeable deflections of response trajectories in the direction of the prime, or covertly, only visible in the delayed onset of movements after response conflicts are solved.[2]

In a simple feedforward system, prime and target signals should traverse the system in ***strict*** succession, i.e., the earliest signal arriving in executive motor areas should carry prime-related information exclusively, with no admixture of target information. In other words, visual signals entering the system in strict succession should generate strictly sequential motor output. The feedforward properties of such a system would show in the time-course of the response: 1) Prime rather than target signals should determine the onset (and initial direction) of the response; 2) target signals should be able to influence the response before it is completed; and, crucially, 3) movement kinematics should initially depend on prime characteristics only and be independent of all target characteristics (***rapid chase criteria***, Schmidt et al., 2006). Note that the rapid-chase criteria do not guarantee that a stimulus-response system is strictly feedforward in all its substages, and they actually do not require such a strict assumption, but they reveal when a system is ***behaviorally equivalent*** to a simple feedforward system. All three criteria were beautifully met by the data in Schmidt et al.'s (2006) study, as well as in comparable studies using pointing movements and LRPs (Schmidt, 2002; Schmidt & Schmidt, 2007; Vath & Schmidt, 2007), linking response priming to sequential feedforward processing of prime and target signals.

Overview of the experiments. In this paper, our goal is to show that visual attention deployed just in time before the presentation of the primes modulates the entire time-course of the unfolding priming effect in a way consistent with modulation of the feedforward processing component, i.e., in accordance with the rapid-chase criteria. In Experiment 1, modulation of the priming effect is induced by spatial precues supposed to summon attention exogenously toward or away from the relevant stimulus positions (Yantis & Jonides, 1990). Experiment 2 extends this result to endogenous precues in a situation where spatial selection is a necessary precondition to performing the task at all, so that all priming effects are conditional on selective attention (***selection for action***; Allport, 1989).

Experiment 1

We employed the primed-pointing procedure developed by Schmidt (2002; Schmidt et al., 2006). Two isoluminant annular targets, one red and one green, appeared in diagonally opposite quadrants of the display (Figure 1, upper panel). Participants pointed from the center of the display to the target of appointed color. Just previous to the targets, there were two primes, one red and one green, at the same two positions. The primes appeared for only 17 ms at prime-target SOAs of 33, 67, or 100 ms. Primes and targets could either correspond in color ***(consistent trials)***, or prime colors could be switched with respect to target colors ***(inconsistent trials)***. Consistent and inconsistent primes were expected to initiate responses into the correct or opposite direction, respectively. Primes were efficiently masked by subsequent targets and hardly visible; participants were not informed about their presence (***metacontrast,*** Breitmeyer & Oğmen, 2006; Francis, 1997). Prime identification performance was not measured explicitly.

--- Insert Fig. 1 ---

Spatially selective attention was manipulated via two exogenous cues that appeared simultaneously 100 ms prior to prime onset (Fig. 1, upper panel). The cues were two annuli centered either on those positions where primes and targets would appear ***(valid trials)*** or on those positions that would remain empty ***(invalid trials).*** The cues were valid in 50 % of the trials and thus unpredictive of stimulus locations or correct responses. We expected that the cues would automatically summon attention to either the stimulus or non-stimulus locations, so that priming could be compared for attended and unattended stimuli.

Methods

Participants. Ten right-handed students from the University of Göttingen (8 female, 2 male, age 19 to 56) with normal or corrected-to-normal vision participated for course credit or for payment of € 24. One additional participant had to be dismissed because he had difficulty distinguishing red from green targets. The experiment was preceded by a flicker photometry task to establish isoluminant colors. Each participant responded to only one color (either red or green, counterbalanced across participants) throughout all sessions. Participants were debriefed after the final session and received an explanation of the experiment. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association.

Apparatus. The experiment was controlled by a 300-Mhz personal computer driving a 14" VGA color monitor (640 by 480 pixel) in synchrony with the monitor retrace rate of 60 Hz. The monitor image was projected onto a workspace via a set of two mirrors, such that participants had the impression that the stimuli appeared directly on the workspace where they could interact with them. The workspace was tilted towards the participant by 44° out of the transversal plane at 70 cm viewing distance. Pointing responses were recorded by a POLHEMUS FASTRAK® magnetic tracking device at a sampling frequency of 120 Hz. The sensor was referenced to the tip of a hand-held stylus, and the workspace was illuminated such that participants could view the hand and stylus superimposed on the stimuli. Participants initiated each trial by placing the tip of the stylus on the fixation point and pressing the space bar with their other hand.

Stimuli. Primes were small disks (diameter 7.6 mm; 1 mm ≈ 0.082° of visual angle) presented against a dark background (0.07 cd/m^2). Targets were annuli with an outer diameter of 15.2 mm and an inner diameter the size of the primes. There was a 83.00 cd/m^2 fixation point (diameter 1.4 mm) in the center of the screen. Green stimuli were desaturated with CIE coordinates of Y = 11.50 cd/m^2, x = .322, and y = .398, while isoluminant red stimuli were matched to the green stimuli by heterochromatic flicker photometry for each participant.

Stimulus conditions occurred equiprobably and pseudorandomly in a completely crossed repeated-measures design.

Procedure. The fixation point appeared after participants had manually initiated the trial. Following a fixation period, attentional cues (diameter 19.0 mm, 83 cd/m^2) were presented in two diagonally opposite quadrants 53.7 mm from fixation (Fig. 1, upper panel). In the ***valid*** 50 % of trials, these were the positions later occupied by primes and targets; in the ***invalid*** 50 % of trials, these were the two empty quadrants. After a cue-prime SOA of 100 ms, one red and one green prime were presented for 17 ms in diagonally opposite quadrants of the display. After a prime-target SOA of 33, 67, or 100 ms, one red and one green target were presented at the same locations as the primes such that their colors were either consistent or inconsistent (switched) with respect to the prime colors. Participants were instructed to point as quickly as possible to the target of appointed color. The period from fixation onset to target onset was fixed at 1000 ms. Targets remained on screen until participants had finished a speeded pointing response towards either target. Participants took part in four experimental sessions, each consisting of one practice block followed by 30 blocks of 24 trials.

Statistical methods. A single session was missing because the participant had been unavailable. Practice blocks were excluded. Trials were excluded if a participant had hit one of the empty target locations, or if arrival times were shorter than 100 ms or longer than 999 ms. The procedure eliminated 0.92 % of all trials. Analyses of variance (ANOVAs) are reported with Greenhouse-Geisser-corrected *p*-values. Generally, only effects meeting a significance criterion of $p < .05$ are reported.

We analyzed the entire time-course of the pointing trajectories, looking at the spatial position of the stylus sensor as a function of time. Pointing trajectories were simplified by projecting the horizontal and vertical coordinates of the stylus tip onto a line connecting the red and green target, counting the starting point as zero and the correct target direction as positive. We established the ***trajectorial priming function*** as a spatio-temporal measure of priming by subtracting trajectories in consistent from those in inconsistent trials (negative values indicating how far the sensor position in inconsistent trials lags behind the sensor position in consistent trials at corresponding points in time). Different aspects of priming can be evaluated by deriving kinematic parameters of the trajectories and the trajectorial priming functions. As a result, we can look at priming effects evaluated at different stages throughout the response, at priming effects in velocity profiles, and various other statistics.

Kinematic parameters were extracted by jackknifing methods (Ulrich & Miller, 2001). Pointing trajectories of the n participants were averaged across each subsample of (n - 1) participants, excluding a different participant from each subsample. Movement parameters (e.g., arrival times and peak velocities) were estimated from each subsample and then averaged, which allows for estimates that are much more reliable than those from single participants. Because each participant's data enter each but one subsample, it can be shown that variances and standard errors of the movement parameters extracted this way are too small by a factor of $(n - 1)^2$ and $(n - 1)$, respectively (Ulrich & Miller, 2001). *F* tests and standard error bars were corrected accordingly to estimate variation among participants rather than subsamples.

Results

Figure 2 (upper panel) shows how the primes affected the trajectories of pointing responses toward the correct target. After the primes and targets had occurred, the sensor remained at rest for a while. Roughly 200 ms after prime onset, it started to move, and on average the movement was directed towards the primes rather than the targets. In consistent trials, this was the correct direction; the sensor traveled continuously in the direction of the correct target until the response was completed. In inconsistent trials, however, the sensor tended to detour into the quadrant specified by the misleading prime before reversing and proceeding in the correct direction. This detour was the longer and reached the further into the wrong quadrant the more time had elapsed between primes and targets.

--- Insert Fig. 2 ---

Priming effects early in the trajectory. We evaluated the priming effect at two points in the unfolding movement: Shortly after movement onset, and shortly before arrival at the correct target location. Priming early in the trajectory was evaluated at the time (from prime onset) when the sensor had first moved at least 3 mm in positive direction.[3] This criterion was crossed earlier in consistent than in inconsistent trials (at crossing times t_{con} and t_{incon}, respectively), $F(1, 9) = 139.36$, $p < .001$, and this ***priming effect (*** $t_{incon} - t_{con}$***)*** increased strongly with prime-target SOA, $F(2, 18) = 43.08$, $p < .001$, reaching values of 150 ms and larger (Fig. 3a). It is obvious from Fig. 2 that these effects mainly reflect the time cost incurred by detours towards the misleading prime. Crossing times increased with SOA, $F(2, 18) = 22.13$, $p < .001$, mainly due to increasing crossing times in inconsistent trials. Importantly, priming effects were larger for valid than for invalid cues, $F(1, 9) = 8.93$, $p = .015$.

Priming effects in arrival times. Arrival times (Fig. 3b) were defined as the times when the sensor first entered a 17-mm radius around the correct target position. They showed the same overall pattern as the priming effects evaluated at the earlier criterion, with earlier arrivals in consistent compared to inconsistent trials, $F(1, 9) = 121.61$, $p < .001$, and a strong increase of priming with SOA, *F*(2, 18) = 165.74, *p* < .001. Again, arrival times increased with SOA, *F*(2, 18) = 161.80, *p* < .001, mainly due to the increase in inconsistent trials. Valid cues led to stronger priming effects than invalid cues, *F*(2, 18) = 37.44, *p* < .001, with additional interactions between validity, consistency, and SOA, *F*(2, 18) = 6.41, *p* = .012, and between validity and SOA, *F*(2, 18) = 6.15, *p* = .017, both indicating a slight deviation from additivity. Response errors (i.e., arrivals at the wrong target location, Fig. 3c) occurred almost exclusively in inconsistent trials, and there the error rates increased with SOA more steeply in valid than in invalid trials.

Priming effects in peak velocities. Overall, priming effects at arrival were markedly smaller than those evaluated at the earlier criterion. This happened because pointing movements in inconsistent trials became faster than those in consistent trials, allowing the inconsistent trajectories to partly catch up with the consistent ones (Fig. 3d). Once the trajectories in inconsistent trials had completed their detour toward the misleading prime, they reached higher peak velocities than those in consistent trials, *F*(1, 9) = 13.68, *p* = .005, and this difference became larger with SOA, *F*(2, 18) = 7.82, *p* = .004. Overall, peak velocity increased with SOA, *F*(2, 18) = 4.56, *p* = .025.

--- Insert Fig. 3 ---

Trajectorial priming effects. Trajectorial priming effects (Fig. 2, lower panel) strongly depended on cue validity and SOA. Onset times of trajectorial priming effects were defined as those times (from prime onset) when the effect first fell below -3 mm (meaning that the sensor position in inconsistent trials lagged at least 3 mm behind that in consistent trials). With increasing SOA, these onset times became shorter, $F(2, 18) = 3.35$, $p = .06$ (Fig. 4a), peak amplitudes of the priming function became more negative, $F(2, 18) = 90.13$, $p < .001$ (Fig. 4b), and the peak velocity of the priming function increased, $F(2, 18) = 31.94$, $p < .001$ (Fig. 4c). With valid compared to invalid cues, peak amplitudes were more negative, $F(1, 9) = 35.34$, $p < .001$, and priming developed at higher velocity, $F(1, 9) = 14.30$, $p = .004$.

--- Insert Fig. 4 ---

Discussion

Our results are in line with previous findings (Schmidt, 2002; Schmidt et al., 2006). On average, responses started at a fixed time following prime onset and initially went into the direction specified by the primes instead of the targets. When primes and targets were consistent, this initial direction was correct, and the sensor simply traveled towards the correct target until the response was completed. When primes and targets were inconsistent, however, the sensor initially traveled into the quadrant occupied by the misleading prime. This detour into the wrong quadrant lasted for a time directly depending on prime-target SOA; then the movements reversed and finally proceeded in the correct direction. As a result, inconsistent primes delayed responses in the correct direction, and these delays increased with prime-target SOA. On average, pointing and priming onsets were strictly time-locked to prime onset even though participants were supposed to respond to the targets, whereas correction movements during inconsistent trials were time-locked to target onset.

Priming effects were clearly affected by cue validity, suggesting modulation by visual attention. Valid as compared to invalid exogenous cues amplified the priming effect early in the trajectory, late in the trajectory, and in the frequency of response errors. Attention modulated the entire time-course of the pointing trajectory: The trajectorial priming function, defined as the spatial difference between consistent and inconsistent trajectories, reached larger peak amplitudes and higher peak velocities in valid compared to invalid trials.

The overall data pattern suggests that pointing responses were controlled sequentially by prime and target signals, such that the response was initiated by the prime and captured in mid-flight by the target signal, as suggested by rapid-chase theory (Schmidt et al., 2003; Vath & Schmidt, 2007). This conclusion is corroborated by the analysis of response errors (i.e., actual arrivals at the incorrect target), which were low in consistent trials where both prime and target activated the correct response, but larger in inconsistent trials where the prime first activated a response in the incorrect direction. Error rates strongly increased with SOA in those trials, presumably reflecting responses that were driven on by the misleading prime signal and failed to be reversed by the target signal before they reached completion.

When inconsistently primed movements finally started to go in the correct direction, they became about 30 % faster than consistently primed movements. This pattern was already observed in earlier studies of primed pointing movements (Schmidt, 2000; Schmidt et al., 2006) and primed LRPs (Vath & Schmidt, 2007). We can offer two explanations. First, the speed-up of inconsistent trajectories might be related to the reversal of response priming effects observed at SOAs beyond 100 ms (Eimer & Schlaghecken, 1998), whereby inconsistent primes lead to ***faster*** responses than consistent ones. Even though the source of this reversal is debated (Lleras & Enns, 2004; Verleger et al., 2004), one explanation is that the prime-initiated response undergoes active self-inhibition (Schlaghecken & Eimer, 2002). Trajectories in inconsistent trials might thus benefit from the earliest effects of self-inhibition of the prime-initiated incorrect response, which in turn might disinhibit the correct response. Second, Vorberg et al.'s (2003) accumulator model of response priming posits two accumulators collecting stochastic sensory evidence for the correct and incorrect response, respectively. The two accumulators inhibit each other, implementing a winner-takes-all system. In the model, information accumulation in the correct direction occurs later but proceeds faster after an inconsistent prime has driven the process in the wrong direction, even without active self-inhibition.

Experiment 2

In Experiment 1, we used attention to modulate the dynamics of a visuomotor task that could just the same have been completed without attentional cues. In Experiment 2, our goal was to create a task where visual selective attention was a necessary precondition for performing the task at all, and also necessary for allowing a priming effect to develop.

We studied the impact of endogenously controlled attention (Yantis & Serences, 2003) on priming by presenting a circular configuration of ten possible targets preceded by ten primes at the same positions (Fig. 1, lower panel). Stimulus configurations were such that neighboring stimuli would be alternatingly red and green, and a red target or prime would always lie opposite to a green one. Participants responded to one pair of opposite targets by pointing to the target of appointed color. To know which of the target pairs to respond to, they had to process a cue presented before prime onset, which indicated the relevant pair of opposing targets. The peculiarity of this design is that primes as well as targets should have a spatially neutral impact on pointing movements unless spatial selection of the cued locations has taken place. Visual selection is thus necessary for performing the task ("selection for action"; Allport, 1989) and for obtaining spatially directed priming effects, not just a modulating influence on performance.

Methods

Participants. Eight right-handed students from the University of Göttingen (7 female, 1 male, age 19 to 25) with normal or corrected-to-normal vision participated for course credit or for payment of € 27.

Procedure. Apparatus and statistical methods were the same as in Experiment 1. Prime and target stimuli were the same as in Experiment 1 but appeared in a new arrangement (Fig. 1, lower panel). The ten possible targets were arranged in a circle 114.0 mm in diameter, such that neighboring targets would be alternatingly red and green, and a red target would always lie opposite to a green one. Similarly, there were 10 colored primes at the same positions with all their colors either consistent or inconsistent (switched) with respect to the target colors. Cues were white bars (83.0 cd/m^2) indicating one pair of opposing targets and extending from the fixation point by 17.8 mm in both directions.

After a fixation period, cues were presented for 50 ms. At a cue-prime SOA ***(cueing interval)*** of either 100, 200, or 500 ms, primes appeared for 17 ms. At a prime-target SOA of either 33, 67, or 100 ms, the targets appeared and remained on screen until participants had finished a speeded pointing response towards the cued target of appointed color or towards any incorrect target. The period from fixation onset to target onset was fixed at 1000 ms. Participants took part in four experimental sessions, each consisting of one practice block followed by 20 blocks of 36 trials. The outlier detection procedure described above eliminated 1.25 % of trials.

Results

Pointing trajectories (Fig. 5, upper panel) were highly similar to those in Experiment 1. On average, the sensor initially started in the direction of the prime and in inconsistent trials continued to detour into the wrong quadrant for a time depending on prime-target SOA. The effect increased with the duration of the cueing period and the prime-target SOA.

--- Insert Fig. 5 ---

Priming effects early in the trajectory. As in Experiment 1, the early criterion (3 mm in positive direction) was crossed earlier in consistent than in inconsistent trials, $F(1, 7) = 81.95$, $p < .001$, and this priming effect increased with prime-target SOA, $F(2, 14) = 31.25$, $p < .001$ (Fig. 6a). Crossing times generally increased with SOA, $F(2, 14) = 27.92$, $p = .001$, mainly due to increasing times in inconsistent trials. Importantly, priming effects also increased with cueing interval, $F(1, 7) = 6.47$, $p = .010$, suggesting that primes had a larger impact on the response when more time was available to select the relevant positions.

--- Insert Fig. 6 ---

Priming effects in arrival times. Arrival times (Fig. 6b) showed the same overall pattern, with earlier arrivals in consistent compared to inconsistent trials, $F(1, 7) = 87.23$, $p < .001$, and a strong increase of this priming effect with SOA, $F(2, 14) = 55.23$, $p < .001$. On average, arrival time increased with SOA, $F(2, 14) = 30.08$, $p < .001$, mainly due to the increase in inconsistent trials. Importantly, priming effects also increased with cueing interval, $F(2, 14) = 35.74$, $p < .001$, as did arrival times in general, $F(2, 14) = 8.97$, $p = .010$. The increase in priming with prime-target SOA was steeper at longer cueing intervals, as confirmed by significant interactions between validity, consistency, and SOA, $F(4, 28) = 7.14$, $p = .002$, and between validity and SOA, $F(4, 28) = 15.27$, $p < .001$. Again, response errors (Fig. 3c) occurred almost exclusively in inconsistent trials, and there increased markedly with SOA and cueing interval.

Priming effects in peak velocities. In contrast to Experiment 1, there was no significant effect of prime-target consistency on peak velocities, $F(1, 7) = 2.09$, $p = .192$ (Fig. 6d). The only noteworthy effects were an increase in peak velocity with cueing interval, $F(2, 14) = 4.46$, $p = .032$, and prime-target SOA, $F(2, 14) = 3.23$, $p = .070$.

Trajectorial priming effects. Trajectorial priming functions (Fig. 5, lower panel) were established as in Experiment 1. Again, their time course strongly depended on cueing interval and prime-target SOA. With increasing SOA, onset times became shorter, $F(2, 14) = 22.32$, $p < .001$ (Fig. 7a), peak amplitudes of the priming function became more negative, $F(2, 14) = 57.19$, $p < .001$ (Fig. 4b), and the peak velocities of the priming function became higher, $F(2, 14) = 57.62$, $p < .001$ (Fig. 4c). Increasing cueing interval had a similar effect on the onset times, peak amplitudes, and peak velocities of the trajectorial priming effects, $F(2, 14) = 5.26$, 29.74, and 8.57, respectively, all $p \leq .020$. The interaction between cueing interval and prime-target SOA was significant only for the peak amplitudes, $F(4, 28) = 7.14$, $p < .001$, which increased more steeply with SOA at longer cueing intervals.

--- Insert Fig. 7 ---

Discussion

Whereas Experiment 1 only demonstrates modulation of a priming effect by visual attention, Experiment 2 employs a selection-for-action paradigm where spatial selection of the relevant locations is a prerequisite for performing the task at all. Priming effects were highly similar to those measured in Experiment 1 and earlier studies (Schmidt, 2002; Schmidt et al., 2006), and clearly increased with cueing interval, suggesting that primes had a higher impact on responses to the targets when more time was available to select the relevant locations. Importantly, priming effects were directional, leading away from the correct target position in inconsistent trials. These detours demonstrate that spatial selection of specific primes must have taken place, because without such selection, primes could not have exerted a spatially directed influence on the pointing response. Even though clear priming effects were observed in arrival times and error rates at a cueing interval as short as 100 ms, these effects nearly tripled in size when the cueing interval was increased to 500 ms. Again, attention modulated the entire time-course of the pointing trajectory: The trajectorial priming function had an earlier onset, reached larger peak amplitudes, and developed with higher peak velocities the longer the cueing interval.

Results suggest that with increasing cueing interval, spatially selective attention more and more efficiently molds into the cued locations (McMains & Somers, 2004). The earlier attention is deployed at selected locations, the more it will enhance visuomotor processing of upcoming stimuli, thereby amplifying the effects of the primes. In contrast, if selection is still incomplete upon arrival of the primes, priming effects will be reduced because the prime display cannot initiate a spatially directed motor response.

General Discussion

Both experiments reported here show that visual attention enhances response priming effects generated by upcoming stimuli. The enhancement encompasses all phases of primed pointing responses: With attention in place, responses start earlier, reach larger peak amplitudes, and can travel with higher peak velocities. The impact of attention can be more than just modulatory: Experiment 2 was designed in a way that spatial selection was necessary not only for performing a spatially directed response, but also for obtaining a spatially directed priming effect.

Does the attentional modulation affect the feedforward component of the pointing task? In behavioral terms, are the priming effects consistent with Schmidt et al.'s (2006) rapid-chase criteria? Regarding only the later prime-target SOAs, the first two of these criteria are met in both experiments: Primes rather than targets determine the onset time and initial direction of the response (criterion 1), and the target signal is able to redirect the response in mid-flight (criterion 2). This data pattern suggests that at these SOAs responses are controlled sequentially by prime and target signals, but does not exclude the possibility that these signals mix or overlap prior to the level of response control. The third criterion therefore evaluates whether primes and targets might control the response in ***strict*** sequence, with no overlap between the signals, so that the initial phase of the priming effect is controlled by a signal containing only prime but no target information. This criterion requires that at each SOA, the trajectorial priming function must display an invariant early time-course – in other words, all curves must initially lie on top of each other and only branch off after following the exact same time-course for a time depending on SOA. The criterion is met for the two later prime-target SOAs in all cueing conditions reported here, which does speak for rapid-chase processing.

However, priming effects at the 33-ms SOA start out too flatly in all conditions, reaching their onset criterion significantly too late (Figs. 4a and 7a), and trajectories at this SOA show no signs of detours into the quadrant of the misleading prime, thus failing all three criteria. There might be several reasons for this departure from the rapid-chase predictions. First, the rapid-chase criteria are defined for ***two*** sequential signals passing through the visuomotor system. Here, we apply them to the second and third of ***three*** signals traversing the system, the first one being the attentional cue. However, this does not explain why the rapid-chase predictions are met at the longer SOAs. Second, rapid chases have to break down at very short prime-target SOAs because the temporal resolution of the system is finite: Ultimately, shorter and shorter SOAs must lead to overlap or mixing of prime and target signals, attenuating the amplitude of the trajectorial priming function right from the start of the response. Up to now, however, we have observed breakdowns of the rapid-chase criteria only for SOAs as short as 17 ms (Schmidt et al., 2006, Exp. 2) but never at longer SOAs (Schmidt, 2002; Schmidt et al., 2006; Schmidt & Schmidt, in prep.; Vath & Schmidt, 2007). -- All things considered, and with some caution applied, our results speak for rapid-chase processing of primes and targets here, at least for the longer SOAs. This outcome supports the idea that the attentional modulation indeed affects the first rapid waves of visuomotor activation, triggered sequentially by primes and targets, that traverse the visuomotor system.

Our general findings are in line with work by other authors. Modulation of response priming by temporal rather than spatial attention has been demonstrated by Naccache, Blandin, and Dehaene (2002) by using Dehaene et al.'s (1998) number priming paradigm. In that study, priming effects occurred only when the onset time of the target was predictable, not when it was embedded in a context of unpredictable onset times, even if the prime-target SOA was preserved. Attentional modulation of semantic priming has been reported by Kiefer and Brendel (2006) and Lachter, Forster, and Ruthruff (2004) with exogenous as well as endogenous spatial cues.

Sumner, Tsai, Yu, and Nachev (2006) studied the effects of exogenous spatial cues on response priming of keypress responses. They presented a sequence of a prime arrow pointing either left or right, a pattern mask, and a target arrow. Primes and targets appeared independently either above or below the fixation point, and attention toward the prime was manipulated by flashing a visual precue 100 ms before prime onset at either the prime's or the opposite location. Consistent with our findings, the magnitude of the priming effect was larger for primes at cued compared to uncued positions. Because the prime-target SOAs employed by Sumner et al. (2006) were much longer than in the present study, in a range where priming effects can actually reverse under suitable stimulus conditions (Eimer & Schlaghecken, 1998, 2003; Lingnau & Vorberg, 2005; Lleras & Enns, 2004; Schlaghecken & Eimer, 2002; Verleger et al., 2004), that study does not fully address the issue how visual attention affects the ***earliest*** visuomotor signals from primes and targets reaching the level of response control.

Nevertheless, Sumner et al.'s (2006) study poses another interesting question. The authors tried to determine whether attentional enhancement reflected a modification of the priming process itself (***motor enhancement***, e.g., by increasing the gain of the motor response or by lowering response thresholds) or an amplification of the prime's signal strength (***signal enhancement***, e.g., by increasing effective signal contrast or signal-to-noise ratio). Sumner et al. (2006) suggested opposite predictions about the respective consequences of different types of enhancement when signal strength was directly varied. A test varying prime duration favored the motor enhancement account but confounded prime duration with prime-target SOA, and the results of a second test eliminating this confound by varying the prime's luminance contrast instead of duration were consistent with signal as well as motor enhancement predictions. The authors concluded that their results could not be explained by signal enhancement alone but implied motor enhancement as well. However, their predictions regarding the effects of prime duration and intensity on the sign and amplitude of the priming effect are difficult to evaluate. Considering possible nonlinearities like mutual inhibition between responses (Vorberg et al., 2003) or even self-inhibition within responses (Schlaghecken & Eimer, 2002), it is difficult to predict the effects of pure signal or motor enhancement without explicitly modeling the full time-course of priming (Lingnau & Vorberg, 2005).

The attentional effects reported here are in line with a signal enhancement interpretation: They are indistinguishable from those obtained by manipulating color contrast directly

(Schmidt et al., 2006), consistent with the idea that visual attention enhances the effective contrast of the prime signal (Boynton, 2005; McAdams & Maunsell, 1999; Reynolds et al., 2000; Reynolds & Chelazzi, 2004; Treue & Martínez Trujillo, 1999). Moreover, we can rule out at least two alternative interpretations. First, the increase in pointing velocities in valid compared to invalid trials speaks against the notion that attention merely *prepones* processing of the prime without changing the subsequent time-course of processing. Second, Experiment 2 rules out the idea that attention has an unspecific (nondirectional) effect on the motor system, e.g., by simply lowering the threshold for *any* upcoming motor response, because our task requires spatial selection of the relevant pair of target locations as a prerequisite for performing the correct response at all.

However, we cannot rule out a third alternative: Attention might play a role in preactivating responses to *both* cued locations while suppressing preparation of responses to uncued locations (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; see also Mathews, Ainsley Dean, & Sterr, 2006; Thompson, Biscoe, & Sato, 2005). But given the large number of demonstrations of attentional enhancement in early visual areas, it seems unlikely that motor enhancement alone is responsible for our results, even though it might well complement any effects of signal enhancement.

Footnotes

[1] In the context of neuronal signal flow, "feedforward" indicates that a cell passes activation on to another cell before integrating any feedback from other cells about that signal (VanRullen & Koch, 2003).

[2] In pointing responses, overt responses in the wrong direction occur mainly in trials with an early movement onset; in the majority of trials, priming is manifest in the delayed onset of responses (Schmidt et al., 2006). These covert processes can be examined electrophysiologically (Vath & Schmidt, 2007). Here we assume that the sequential response activation processes at work are identical for overt and covert priming effects.

[3] Note that in many inconsistent conditions, this criterion could only be reached ***after*** any detour in negative direction. Therefore, it is not strictly a criterion of movement onset. It was not possible to properly calculate onset times in negative direction because detours were not always large enough to yield such a measure.

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Figure captions

Fig. 1. Stimuli and tasks. In Experiment 1 (upper panel), attentional cues were flashed either in the two quadrants where primes and masks would appear (***valid cues,*** solid circles) or in the remaining quadrants (***invalid cues,*** dashed circles). In Experiment 2 (lower panel), ten primes and ten possible targets were presented, and the relevant locations of primes and targets were indicated by a white bar. Both panels depict inconsistent trials where primes and targets at corresponding conditions have opposite colors. Light and dark gray indicate isoluminant red and green colors, respectively. See text for further details.

Fig. 2. Upper panel: Pointing trajectories in Experiment 1. The dependent variable is the position of the sensor projected onto the target-nontarget line, zero denoting the fixation point, positive values denoting the correct-target direction. The time axis is locked to prime onset so that dashed vertical lines denote the possible times of target onset. Lower panel: Trajectorial priming functions obtained by subtracting consistent from inconsistent trajectories. Negative values indicate that the sensor position in inconsistent trials lags behind that in consistent trials. Vertical stippled lines indicate possible target onset times; horizontal stippled lines indicate the various evaluation criteria.

Fig. 3: Parameters of pointing trajectories: Time to an early criterion (upper left), time to arrival (upper right), error rate (lower left), and peak velocity (lower right). The early criterion is located on a radius 3 mm from fixation, in the direction of the correct target. The arrival criterion is located on a radius 17 mm around the correct target. All times are from prime onset. Here and in all subsequent figures, error bars denote the standard error of the mean estimated from jackknifed data (Ulrich & Miller, 2001), corrected for between-subjects variance (Loftus & Masson, 1994).

Fig. 4: Parameters of trajectorial priming functions. Time to priming onset (left), peak amplitude of the priming function (center), and peak velocity of the priming function (right). Priming onset is defined as the point in time where the priming functions first falls below -3 mm. All times are from prime onset.

Fig. 5: Trajectories (upper panel) and trajectorial priming functions (lower panel) in Experiment 2. Conventions as in Fig. 2.

Fig. 6: Parameters of pointing trajectories. Conventions as in Fig. 3 except that the arrival criterion is on a radius of 15 mm around the correct target.

Fig. 7: Parameters of trajectorial priming functions. Conventions as in Fig. 4.

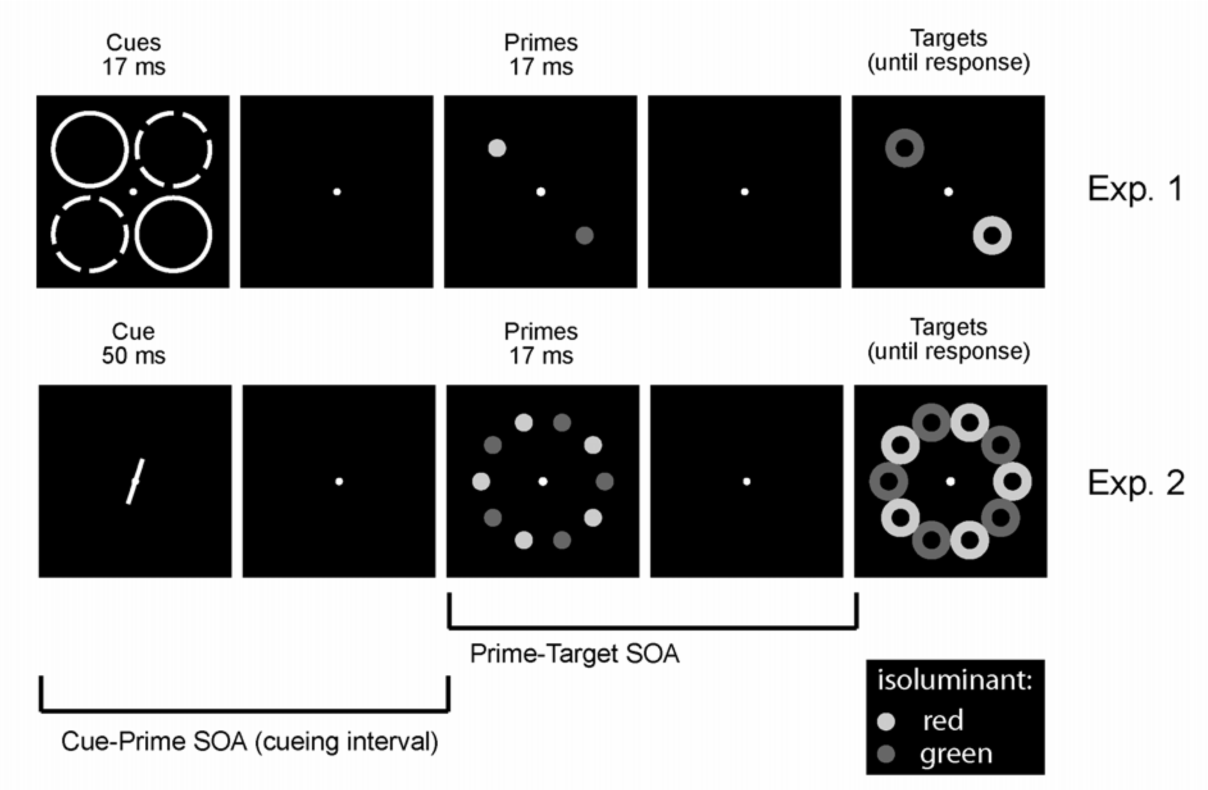
Cues
17 ms
Primes
17 ms
Targets
(until response)
Exp. 1
Cue
50 ms
Primes
17 ms
Targets
(until response)
Exp. 2
Prime-Target SOA
Cue-Prime SOA (cueing interval)
isoluminant:
red
green

Fig. 1

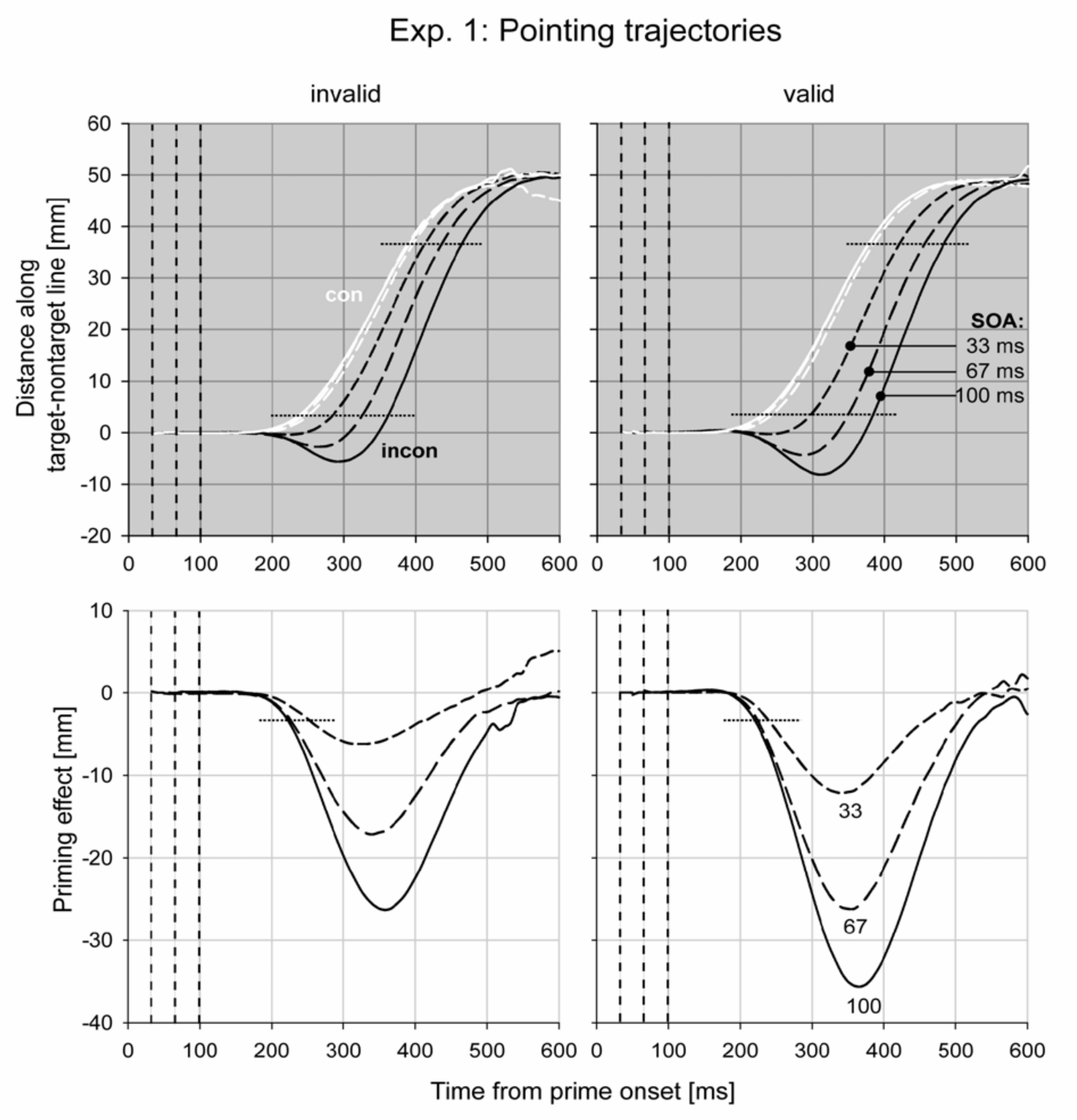
Exp. 1: Pointing trajectories
invalid
valid
Distance along target-nontarget line [mm]
60
50
40
30
20
10
0
-10
-20
con
incon
SOA:
33 ms
67 ms
100 ms
0
100
200
300
400
500
600
Priming effect [mm]
10
0
-10
-20
-30
-40
33
67
100
Time from prime onset [ms]

Fig. 2

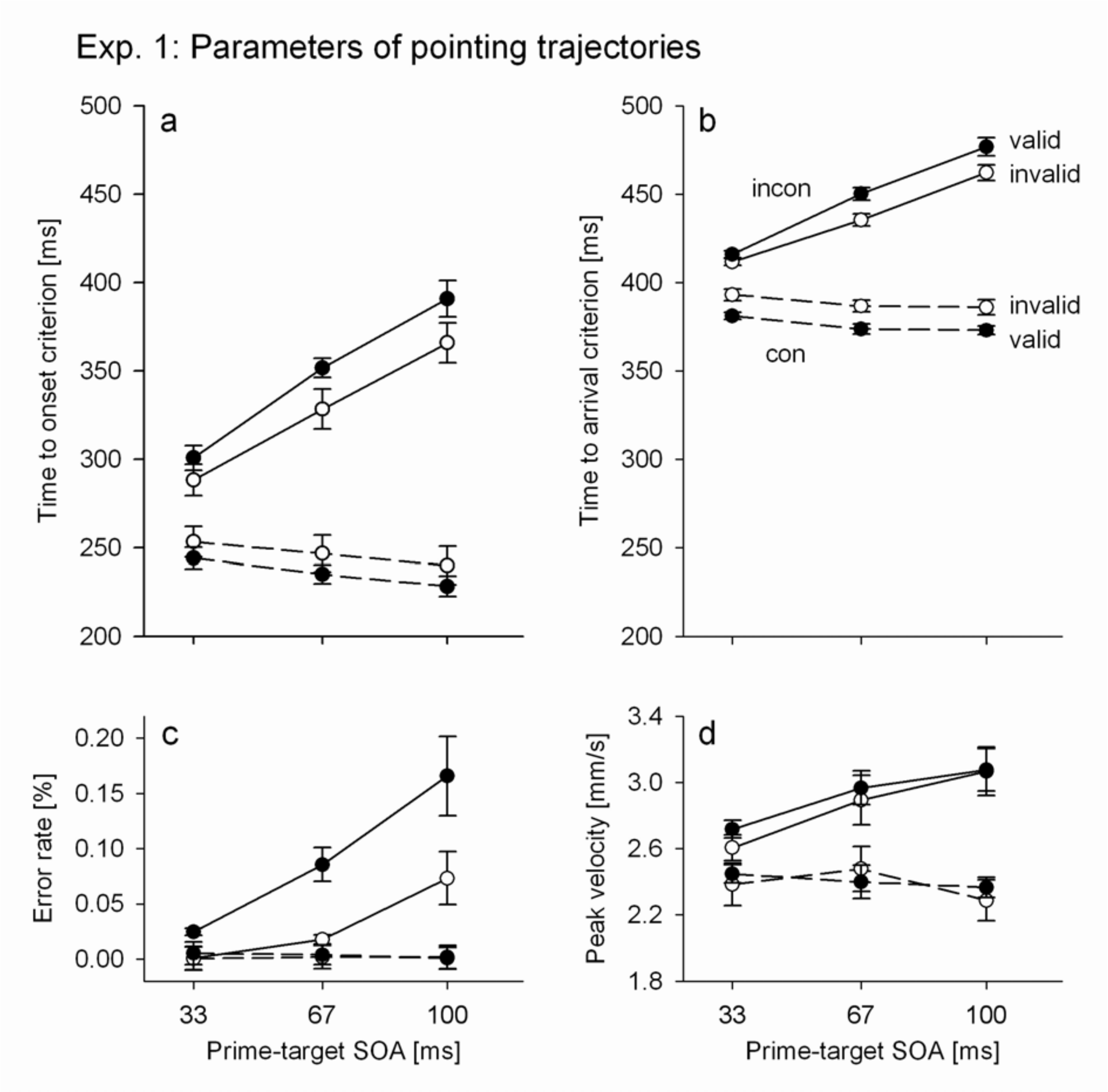
Exp. 1: Parameters of pointing trajectories
a
Time to onset criterion [ms]
500
450
400
350
300
250
200
b
Time to arrival criterion [ms]
incon
con
valid
invalid
invalid
valid
c
Error rate [%]
0.20
0.15
0.10
0.05
0.00
d
Peak velocity [mm/s]
3.4
3.0
2.6
2.2
1.8
33
67
100
Prime-target SOA [ms]

Fig. 3

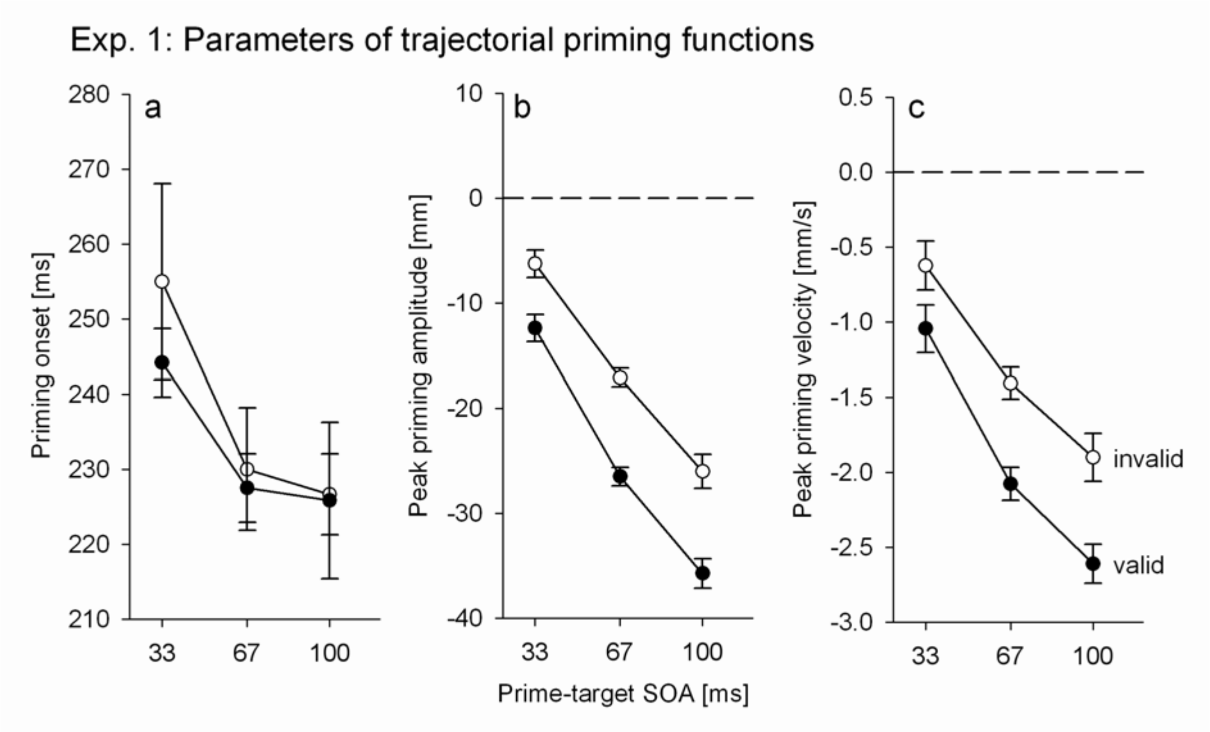
Exp. 1: Parameters of trajectorial priming functions
a
Priming onset [ms]
280
270
260
250
240
230
220
210
b
Peak priming amplitude [mm]
10
0
-10
-20
-30
-40
c
Peak priming velocity [mm/s]
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
33
67
100
Prime-target SOA [ms]
invalid
valid

Fig. 4

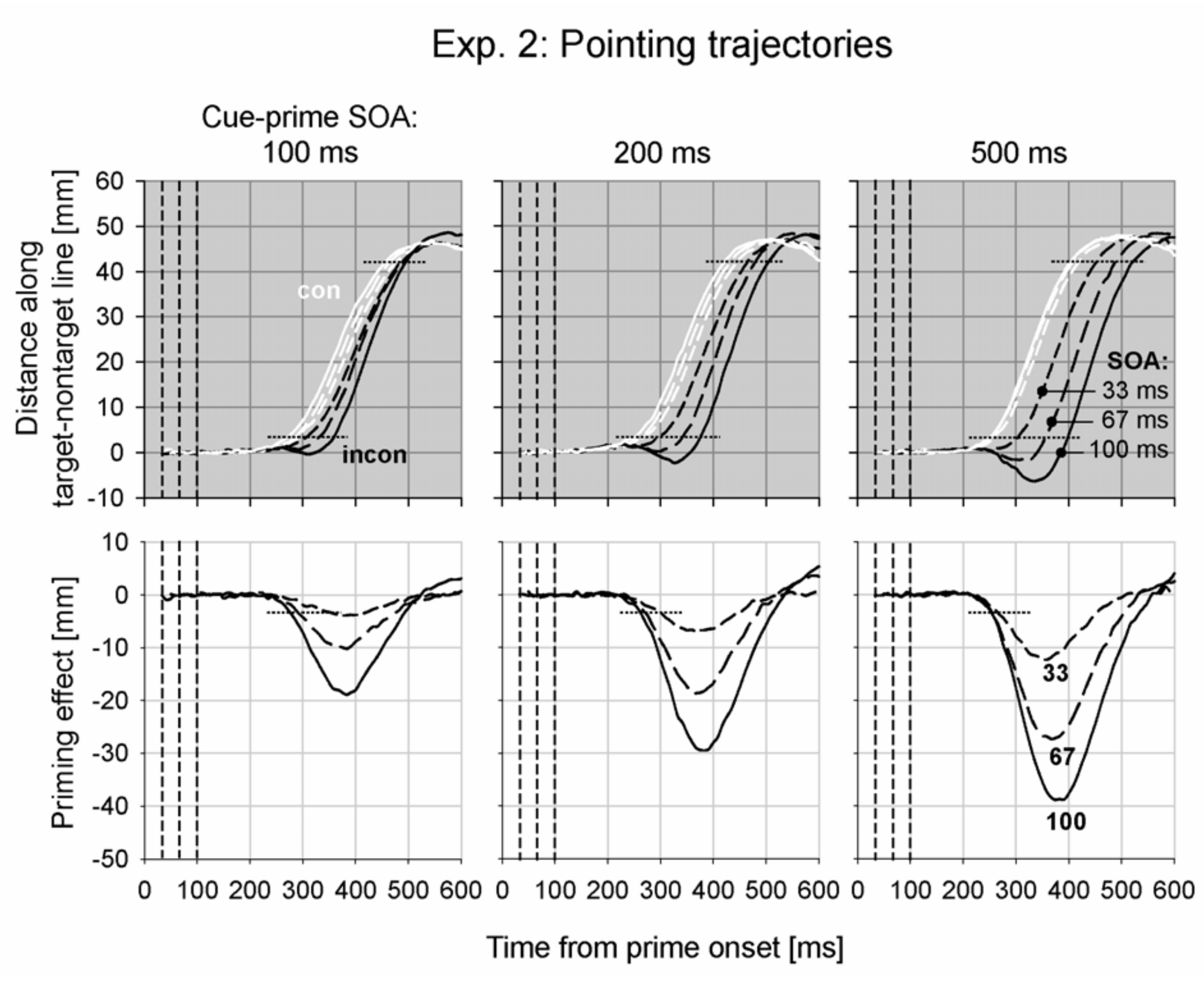
Exp. 2: Pointing trajectories
Cue-prime SOA:
100 ms
200 ms
500 ms
Distance along target-nontarget line [mm]
60
50
40
30
20
10
0
-10
con
incon
SOA:
33 ms
67 ms
100 ms
Priming effect [mm]
10
0
-10
-20
-30
-40
-50
33
67
100
0
100
200
300
400
500
600
Time from prime onset [ms]

Fig. 5

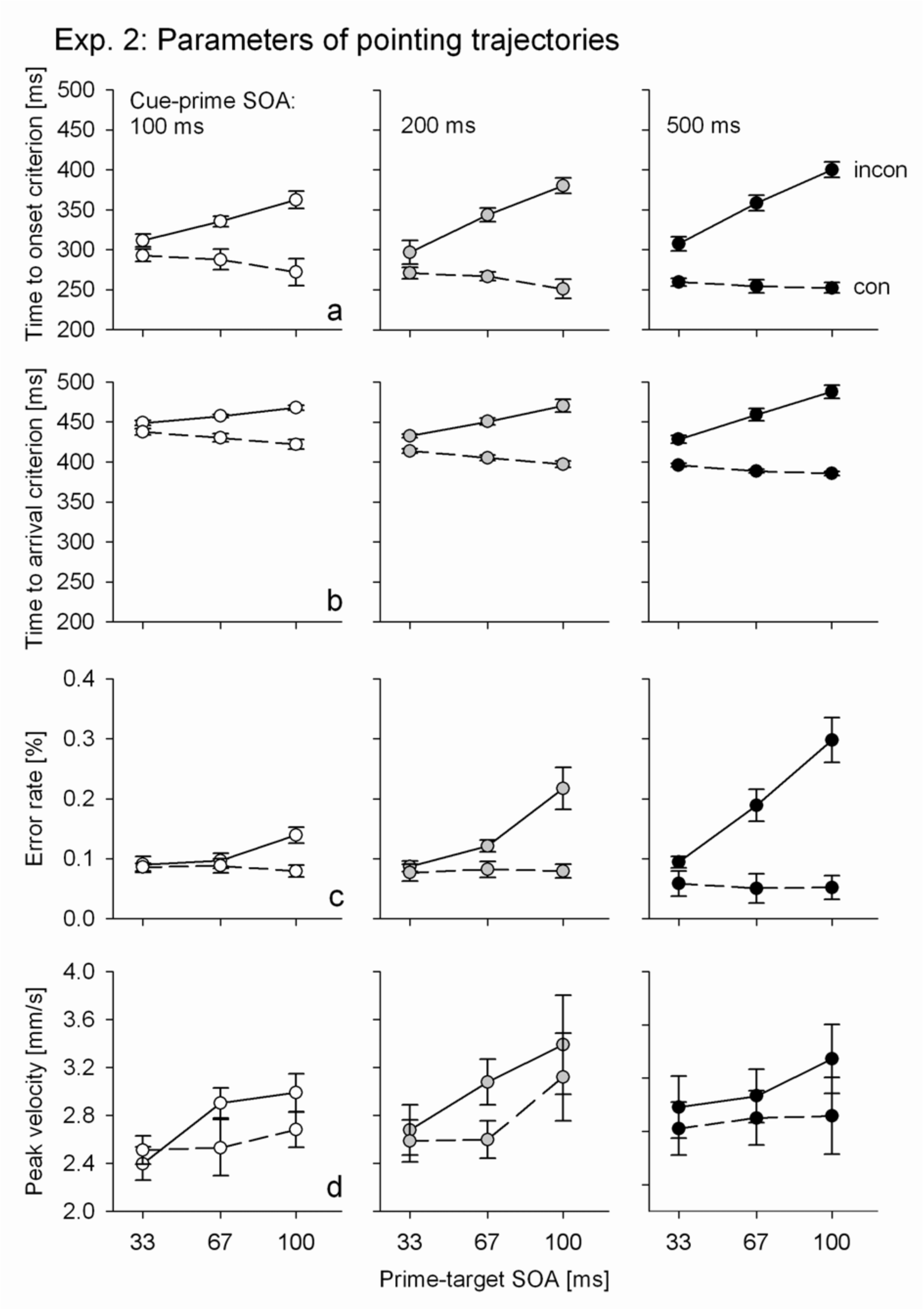
Exp. 2: Parameters of pointing trajectories
Cue-prime SOA: 100 ms
200 ms
500 ms
incon
con
Time to onset criterion [ms]
500
450
400
350
300
250
200
a
Time to arrival criterion [ms]
500
450
400
350
300
250
200
b
Error rate [%]
0.4
0.3
0.2
0.1
0.0
c
Peak velocity [mm/s]
4.0
3.6
3.2
2.8
2.4
2.0
d
33
67
100
Prime-target SOA [ms]

Fig. 6

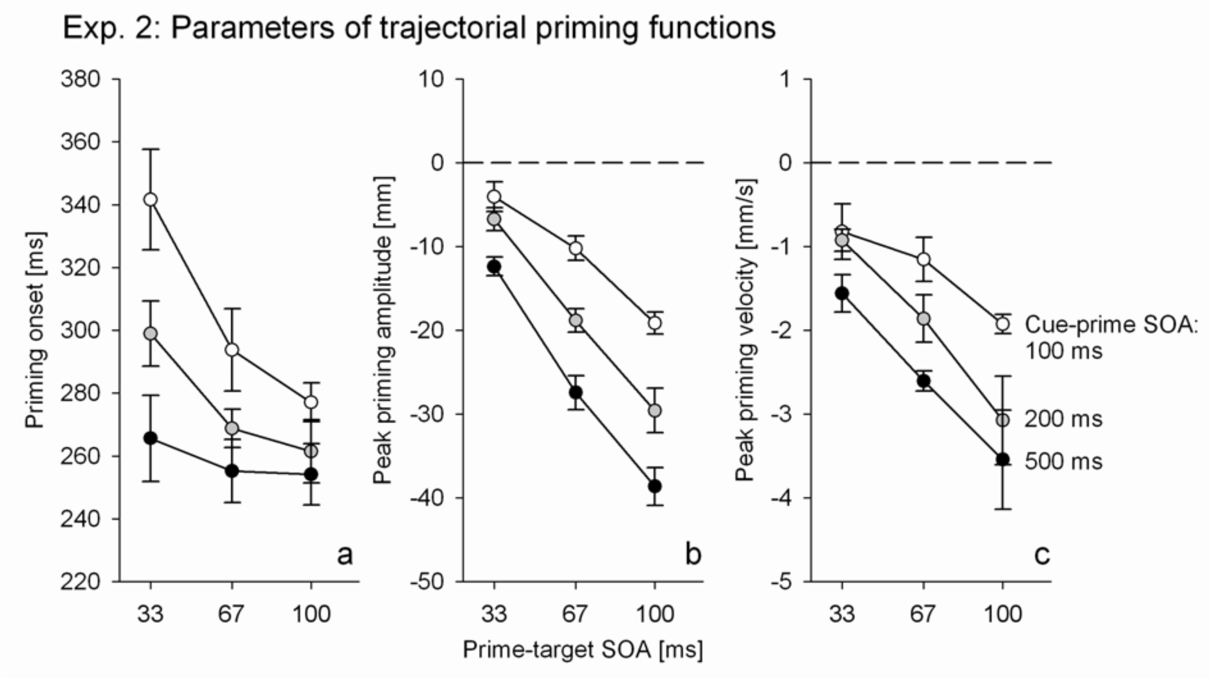
Exp. 2: Parameters of trajectorial priming functions
Priming onset [ms]
380
360
340
320
300
280
260
240
220
a
Peak priming amplitude [mm]
10
0
-10
-20
-30
-40
-50
b
Peak priming velocity [mm/s]
1
0
-1
-2
-3
-4
-5
c
Cue-prime SOA:
100 ms
200 ms
500 ms
33
67
100
Prime-target SOA [ms]

Fig. 7