

TRACING SEQUENTIAL WAVES OF RAPID VISUOMOTOR ACTIVATION IN LATERALIZED READINESS POTENTIALS

N. VATH^{a*} AND T. SCHMIDT^b

^aUniversity of Göttingen, Department of Psychology, Gosslerstr. 14, D-37073 Göttingen, Germany

^bUniversity of Giessen, Department of Cognitive Psychology, Otto-Behaghel-Str. 10F, D-35394 Giessen, Germany

Abstract—Feedforward activation processes are widely regarded as crucial for the automatic initiation of motor responses, whereas recurrent processes are often regarded as crucial for visual awareness. Here, we used a set of behavioral criteria to evaluate whether rapid processing in the human visuomotor system proceeds as would be expected of a feedforward system that works independent of visual awareness. We measured lateralized readiness potentials (LRPs) for key-press responses to color targets (“masks”) preceded by masked color primes mapped onto the same or opposite response, and traced the time-course of motor activation as a function of different prime and mask characteristics. LRP time-courses showed that initial motor activation occurred in prime direction and was time-locked to prime onset. Response activation was then captured on-line by the mask signal, with motor activation now time-locked to the mask and proceeding in mask direction. Crucially, the time-course of early activation by the prime was independent of all mask characteristics. This invariance in early priming effects contrasted with large differences in visual awareness for the prime produced by different masks. Results suggest that primed responses to color stimuli are controlled by feedforward waves of activation sequentially elicited by prime and mask signals traveling rapidly enough to escape the recurrent processes leading to backward masking. © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

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An outstanding feature of the visual system is the two-way organization of information processing. Feedforward projections that proceed from early (sensory) processing stages to later (e.g. motor) ones can be distinguished from feedback connections that go in the opposite direction (Felleman and Van Essen, 1991; Salin and Bullier, 1995). However, the extent to which computational loops participate in different visual functions is still discussed controversially.

Arguing from a meta-analysis of single-cell recordings, Lamme and Roelfsema (2000) concluded that a sudden

visual stimulus initiates a wave of feedforward activation that travels through the brain so rapidly that a cell first reached by the wave front of this *fast feedforward sweep* can respond only on the basis of its current state, i.e. its classically defined receptive field, and would at that time be part of a pure feedforward cascade. Similarly, studies in rapid stimulus classification by human observers suggest that most of the stimulus-relevant information could be extracted from the temporal distribution of the very first spikes in the feedforward wave front (Kirchner and Thorpe, 2006; Rousset et al., 2002; Thorpe et al., 1996; VanRullen and Koch, 2003; VanRullen and Thorpe, 2002). At the same time, many authors assume that feedforward processing alone is insufficient to generate visual awareness of a stimulus and that a stimulus must be processed recurrently to become consciously accessible (e.g. Lamme, 2002, 2004; Lamme and Roelfsema, 2000; Tong, 2003). For instance, studies in visual backward masking suggest that the masked stimulus is degraded by recurrent activity before it reaches awareness (Bacon-Macé et al., 2005; DiLollo et al., 2003; Lamme et al., 2002; Macknik and Haglund, 1999), and studies using transcranial magnetic stimulation suggest that visual awareness of a stimulus is suppressed if feedback loops from extrastriate visual areas through primary visual cortex are disrupted at critical points in time (Pascual-Leone and Walsh, 2001; Ro et al., 2003).

The hypothesis of a fast feedforward sweep in human vision is controversial, because feedback mechanisms in early visual areas can be very rapid (Bullier, 2001; Girard et al., 2001; Panzeri et al., 2001), and there are many possibilities for signals processed in parallel visual streams to cross or overtake each other well before the first overt signs of motor activation might occur (Merigan and Maunsell, 1993; Van Essen and Anderson, 1995). Schmidt et al. (2006) proposed a set of behavioral criteria to evaluate whether rapid processing in the visuomotor system proceeds as would be expected of a feedforward system, focusing on the input–output dynamics of the system as a whole instead of assuming purely feedforward processing in all its subcomponents. They introduced the concept of a rapid chase, which applies to visuomotor tasks where sequential visual stimuli run for control of the same speeded motor response. If sequential signals are engaged in a rapid chase, they will take strictly sequential control over the same motor response, such that the response will initially be controlled by the first stimulus alone.

By Schmidt et al.'s (2006) definition, two successive visuomotor stimuli S_1 and S_2 (S_1 preceding S_2) give rise to a rapid-chase process if the time course of motor output meets the following requirements (rapid-chase criteria).

*Corresponding author. Tel: +49-551-39-3612; fax: +49-551-39-3662. E-mail address: nvath@uni-goettingen.de (N. Vath), thomas.schmidt@psychol.uni-giessen.de (T. Schmidt).

Abbreviations: ANOVA, analysis of variance; EEG, electroencephalogram; LRP, lateralized readiness potential; Mask ID, mask identification task; PLRP, priming effect in lateralized readiness potential; Prime ID, prime identification task; SOA, stimulus onset asynchrony.

Firstly, the response must be initiated by S_1 , such that the onset of the response is time-locked to the onset of that stimulus and starts in the direction specified by it. Secondly, the response must be influenced by S_2 before running to completion, such that the trajectory of the response changes in accordance with S_2 for some time before the end of the response. (Together, these two criteria ensure that the time order of motor output matches the time order of the stimuli controlling that output.) Thirdly, the response to S_1 must initially be independent of S_2 , such that the early parts of the motor trajectory depend only on properties of S_1 , but are invariant with respect to all properties of S_2 . This third criterion ensures that the motor output elicited by sequential stimuli not only preserves the stimulus sequence but is strictly sequential, as would be expected from a feedforward system with temporal resolution high enough to transmit signals with little or no temporal overlap. Failure to meet the third criterion (i.e. if even the earliest parts of the trajectory depend on S_2 as well as S_1) would indicate that the signals mix or overlap in time before the motor output is generated. Even though such a system could still be a feedforward system with low temporal resolution, its feedforward properties would not be apparent in the motor output. Schmidt et al. (2006) investigated priming effects in pointing movements (Schmidt, 2002) and found the data to meet all three rapid-chase criteria.

The purpose of the following experiment was to establish the existence of rapid-chase processes on a physiological basis by tracing the time-course of lateralized readiness potentials (LRPs). The LRP represents the relative increase in electroencephalogram (EEG) negativity over the motor cortex contralateral to an upcoming movement and can be regarded as reflecting response preparation (e.g. Leuthold et al., 2004). We used a *response priming* paradigm (Klotz and Neumann, 1999; Neumann and Klotz, 1994; Vorberg et al., 2003) to investigate rapid-chase processing because there is strong evidence that this paradigm involves rapid response activation that is independent of visual awareness. Vorberg et al. (2003) had participants perform key-press responses to the direction of large arrow masks preceded by small arrow primes whose pointing direction could be either the same as the mask's (*consistent primes*) or opposite to the mask's (*inconsistent primes*). The large arrows served a dual purpose (Neumann and Klotz, 1994): They were the targets for the key-press response, and also served to reduce the visibility of the primes by metacontrast, a form of visual backward masking (Breitmeyer and Ogmen, 2006; Francis, 1997). Responses were speeded by consistent primes and slowed by inconsistent primes, and the magnitude of this *response priming effect* increased linearly with the stimulus onset asynchrony (SOA) of prime and mask. Strikingly, the time-course of priming was independent of the visibility of the prime: The increase in priming with SOA was invariant no matter whether the prime could be identified perfectly or not at all, and no matter whether identification performance increased or decreased with SOA (see also Mattler, 2003; Schmidt and Vorberg, 2006). Results from psychophysiological and imaging studies have shown in

similar paradigms that primes directly trigger the specific motor responses assigned to them, leading to elicitation of LRPs (Eimer and Schlaghecken, 1998, 2003; Leuthold and Kopp, 1998) as well as lateralized metabolic motor activity (Dehaene et al., 1998; see Henson, 2003, for a review).

EXPERIMENTAL PROCEDURES

We employed a variant of the response priming paradigm where participants performed speeded responses to the color of a ring-shaped metacontrast mask that was either red or green, with a masked red or green prime appearing in the central cutout of the mask just prior to its onset (Fig. 1; Schmidt, 2000, 2002). To be able to disentangle the relative contributions of prime and mask signals to the LRP at various points in time, we manipulated the feedforward dynamics of primes and masks by independently varying their color saturation while leaving their subjective luminance constant. In addition, we varied the prime–mask SOA to see which of the LRP components would time-lock to prime and mask signals, respectively. We expected response priming effects to follow the rapid-chase criteria, so that the earliest signs of response activation should exclusively depend on properties of the prime and be strictly time-locked to its onset. In contrast, later phases of response activation should be captured on-line by the mask signal and therefore be time-locked to its onset. Importantly, the response activation evoked by the primes should initially be independent of all properties of the mask.

Participants

Eight right-handed students from the University of Göttingen (two male, six female, aged 22–30 years) participated in six 90-minute sessions for course credits or for a payment of €8 per hour. Each participant had a normal EEG and normal or corrected-to-normal

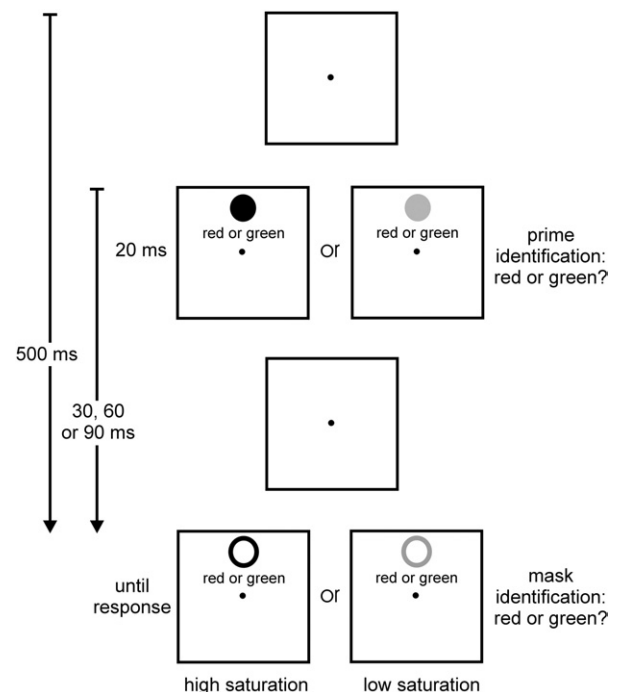


Fig. 1. Experimental procedure. Primes as well as masks could be independently presented in red or green. All colors were isoluminant to the same standard gray. Light and dark gray tones in the figure symbolize low and high color saturation, respectively.

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