Intentional and Unintentional Contributions to Nonspecific Preparation: Electrophysiological Evidence

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The authors hypothesized that there are distinct intentional and unintentional influences on nonspecific preparation for a future event. In 2 experiments, participants responded to an imperative stimulus (S_2) that was presented equiprobably either 400 ms or 1,200 ms after the offset of a warning stimulus (S_1). During the S_1–S_2 interval, the authors measured the contingent negative variation (CNV), an event-related brain potential reflecting nonspecific preparation. S_1 provided either no information or reliable information about the duration of the impending S_1–S_2 interval, thereby allowing an intentional influence on the state of preparation. The effect of S_1 information on the CNV was approximately additive to the effect of the S_1–S_2 interval that was used on the preceding trial. This supports the view that the preceding S_1–S_2 interval contributes unintentionally to the state of nonspecific preparation guided by a process of trace conditioning.

There is little doubt that human and animal behavior is a joint function of intentional and unintentional influences. Intentional influences stem from a goal-oriented, optional plan of the organism and therefore have an internal origin. Influences unrelated to this plan are unintentional. These influences are typically triggered by events in the outside world but may be modified by a past learning history of the organism.

In the present study, we examined intentional and unintentional influences on nonspecific preparation. Nonspecific preparation is concerned with the fluctuations of general preparedness for action to an anticipated event (e.g., Niemi & Näätänen, 1981). Recent investigations have yielded preliminary evidence for two possible contributions to nonspecific preparation, here referred to as *temporal orienting* (Coull, Frith, Büchel, & Nobre, 2000; Nobre, 2001) and *trace conditioning* (Los, Knol, & Boers, 2001; Los & Van den Heuvel, 2001). The contribution of temporal orienting relies on an intentional act of preparation, which comes to the fore when a participant is informed about the timing of an impending event. The contribution of trace conditioning is unintentional and is determined by the temporal layout of events on the trials that immediately precede the current trial. In this study, we present electrophysiological data that justify this distinction between temporal orienting and trace conditioning. In addition, we present a framework that shows how these influences may combine to affect behavior.

Temporal Orienting: An Intentional Influence to Nonspecific Preparation

Evidence for separate contributions of temporal orienting and trace conditioning to nonspecific preparation stems from studies with the variable-foreperiod design. In this design, participants respond as quickly as possible to an imperative stimulus (S_2) that follows a warning stimulus (S_1) after an interstimulus interval, referred to as the foreperiod (FP). When FP varies at distinct levels across the trials of a single block, S_2 can occur at one of several moments after S_1 has turned off. These moments are here referred to as *critical moments*. The moment that is used for the presentation of S_2 on any given trial is referred to as the *imperative moment* of that trial. In the variable-foreperiod design, the participant's reaction time (RT) has been shown to be dependent on FP. In particular, under a uniform distribution of FPs (i.e., when each possible FP has an equal probability of being used on each trial), the classical finding is that as FP lengthens, RT decreases according to a negatively accelerating function (e.g., Niemi & Näätänen, 1981; Woodrow, 1914). This finding is here referred to as the classical FP–RT function.

The possible influence of temporal orienting on the state of nonspecific preparation can be readily demonstrated within the outlines of this design. In particular, when a symbolic cue presented prior to S_1 (or as an integral part of S_1) provides valid information about the duration of the impending FP, participants can use this information to speed up their subsequent response to S_2. Because this speedup is much more pronounced when the cue specifies an early critical moment than when it specifies a late critical moment, cuing causes a considerable flattening of the classical FP–RT function (e.g., Coull et al., 2000; Kingstone, 1992, Experiment 4; Los & Van den Heuvel, 2001; Mo & Kersey, 1980; Zahn, 1970). Thus, by means of an intentional act, participants appear to be capable of enhancing their preparedness for action, especially at those critical moments at which their state of preparation tends to be low.

In view of this finding, it is natural to also assign a central role to temporal orienting in accounting for the classical FP–RT function when no cue is presented. One proposal has been that temporal orienting develops in accordance with the conditional probability of S_2 occurrence after the presentation of S_1. Given a uniform distribution of FPs, this conditional probability is low at outset and

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increases monotonically as critical moments are bypassed without the occurrence of S_2 to reach unity just prior to the last critical moment. If the strength of temporal orienting and ensuing nonspecific preparation develops in accordance with this conditional probability, the classical FP–RT function readily follows. Support for this view stems from the observation that the FP–RT function becomes flat when a nonaging distribution of FPs is used, such that the conditional probability of S_2 occurrence is constant after S_1 (e.g., Näätänen, 1971; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000). Perhaps for this reason, the idea that temporal orienting is driven by the conditional probability of S_2 occurrence has been very influential (e.g., Luce, 1986; Sperling & Dosher, 1986).

However, in spite of its parsimony, this account has a major shortcoming: It fails to acknowledge that the FP–RT function has limited significance in itself but derives its existence, at least to a large extent, from sequential effects of FP. These sequential effects entail that the RT on a given trial n is longer when the FP of that trial (FP_n) is shorter than the FP of the preceding trial (FP_{n-1}) relative to when it is as long as or longer than FP_{n-1} (e.g., Baumeister & Joubert, 1969; Elliot, 1970; Karlin, 1959; Los et al., 2001; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004; Woodrow, 1914; Zahn, Rosenthal, & Shakow, 1963). Stated differently, RT on trial n is longer when the imperative moment of that trial was bypassed during FP_{n-1} than when it was not bypassed during FP_{n-1}. Note that these sequential effects are highly asymmetric, in the sense that relative to an intertrial repetition of FP, costs in RT are observed when FP_n is shorter than FP_{n-1} but not vice versa. This asymmetry has a crucial implication for the classical FP–RT function: This function reflects to a large extent differential sequential influences on mean RT at early and late critical moments. Specifically, as a critical moment occurs later relative to other critical moments, it is less frequently bypassed during FP_{n-1} and, therefore, gives rise to a shorter mean RT. The consequence is that the classical FP–RT function should not be studied isolated from the sequential effects that give rise to it (Los et al., 2001).

Given the primacy of sequential effects of FP, it is still possible to assign a central role to temporal orienting, as indicated by Niemi and Näätänen (1981) and Requin, Brener, and Ring (1991). Their proposal, here referred to as the *reorienting account*, begins with the assumption that at the start of each trial, participants engage in a strategy of orienting to the critical moment that was the imperative moment on the last trial. This strategy enables participants to respond quickly to S_2 not only when the expected critical moment turns out to be the imperative moment on that trial but also when the imperative moment occurs later than the expected critical moment. In the latter case, participants will notice their incorrect temporal orienting in due time and reorient to a later critical moment prior to the presentation of S_2, thus averting an RT deficit. By contrast, an RT deficit cannot be averted when S_2 occurs earlier than the expected critical moment, because participants will notice their incorrect temporal orienting only after the presentation of S_2, when they are caught in a state of low preparation. In sum, while maintaining a central role of temporal orienting, this proposal accounts for the asymmetry of sequential effects and, indirectly, for the classical FP–RT function.[1]

Trace Conditioning: An Unintentional Contribution to Nonspecific Preparation

Taking a different theoretical viewpoint, Los and colleagues (Los, 1996, 2004; Los et al., 2001; Los & van den Heuvel, 2001) attributed sequential effects of FP to the dynamics of classical (or operant) trace conditioning. Classical conditioning refers to an associative learning process in which an organism acquires an adaptive conditioned response (CR) to an initially neutral conditioned stimulus (CS) as it learns the contingency between the CS and a threatening or rewarding unconditioned stimulus (US). The distinctive feature of the trace-conditioning paradigm is that a blank interval, or trace, separates the offset of CS from the onset of US. After the organism has learnt the CS–US contingency, the primary interest of this paradigm concerns the within-trial development of the CR as a function of time since the onset of CS. The basic finding is that on test trials on which the US is omitted, the average CR shows a bell-shaped function of time since the onset of CS, with its peak aligned to the moment at which US normally occurs (for reviews, see, e.g., Gallistel & Gibbon, 2000; Roberts, 1998). Thus, by showing that the CR is adaptively timed to the moment of US occurrence, this paradigm holds the promise of revealing crucial information on the timing capabilities of the organism.

Los (1996) noted that the variable-foreperiod design is formally equivalent to the design used in trace conditioning, which becomes evident when S_1 is substituted for CS and S_2 for US, in which case FP constitutes the trace (i.e., the blank CS–US interval). The fact that S_2 has no intrinsic biological relevance to the organism in the FP design, contrary to the US in typical conditioning designs, is probably relatively unimportant. In fact, biological relevance is not a prerequisite for conditioning, as evidenced by effective associative learning occurring in preconditioning and second-order conditioning paradigms (e.g., Gallistel & Gibbon, 2000). Furthermore, in contemporary treatises of conditioning, the contents of events are considered of less importance than their timing (Gallistel & Gibbon, 2000). In view of these considerations, it is straightforward to pursue the possibility of accounting for sequential effects of FP in terms of trace conditioning.

To evaluate the merits of this framework for understanding human nonspecific preparation, it is useful to start with the simplifying assumption that the state of nonspecific preparation is identical to a state of conditioning. In that case, S_1, in the quality of a CS, elicits the peaks and troughs in this state of conditioning as FP develops. In accordance with a set of learning rules, the state of conditioning corresponding to each critical moment is dynamically adjusted during FP and preserved for the next trial. One simple set of rules (e.g., Los, 1996, 2004; Los et al., 2001; Los & Van den Heuvel, 2001) implies that (a) the state of conditioning corresponding to any critical moment is lowered (i.e., subject to

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[1] A reviewer of a prior version of this article correctly pointed out that accounts of FP effects in terms of either conditional probability or (what we call) reorienting need not necessarily rely on intentional temporal orienting. In fact, most authors have used the concept of temporal expectancy instead of temporal orienting, taking a more neutral position on the intentional–unintentional dimension. Yet we feel our exposition is adequate, because the literature of (sequential) effects of FP is permeated with strategic notions (cf. Los & Van den Heuvel, 2001).

extinction) as that moment is being bypassed during FP, (b) the state of conditioning corresponding to the imperative moment is enhanced (i.e., reinforced) when the response to S_2 is released, and (c) the state of conditioning corresponding to any critical moment beyond the imperative moment is left unchanged. Because the influence of extinction is limited to critical moments prior to the imperative moment, the asymmetry of sequential effects follows, and hence the classical FP–RT function (for further details, see Los et al., 2001; Los & Van den Heuvel, 2001).

In a formal analysis, Bosse, Jonker, Los, Van der Torre, and Treur (2004) have shown that, within reasonable limits, the learning rules of this model are global properties of the formal model developed by Machado (1997) to account for animal timing behavior. In addition, Los et al. (2001) have shown that a variant of Machado's model fits well to an extensive pattern of RT data involving first-order and second-order sequential effects in a mixed presentation of FPs, as well as main effects of FP in pure blocks (i.e., when the same FP is used on each trial of a block). Thus, trace conditioning may provide a detailed account of key phenomena of nonspecific preparation while ensuring excellent coherence with the literature on animal timing (e.g., Machado, 1997; Machado & Keen, 1999).

A Single-Path Hypothesis and a Dual-Path Hypothesis

From the preceding sections, it transpires that there is consensus on the status of cuing effects as reflecting intentional temporal orienting (e.g., Coull et al., 2000; Los & Van den Heuvel, 2001; Nobre, 2001) but not on the status of sequential effects. According to the reorienting account, sequential effects also reflect a strategic use of temporal orienting, whereas according to the conditioning account, sequential effects stem from an unintentional application of temporal learning rules (Los & Van den Heuvel, 2001). Thus, the reorienting account of sequential effects is consistent with a *single-path hypothesis*, in which all phenomena of nonspecific preparation reflect the application of temporal orienting. If no cue provides information about the duration of the impending FP, temporal orienting is guided by the imperative moment of the preceding trial; if there is a cue, temporal orienting is guided by the contents of the cue instead. However, the trace-conditioning account of sequential effects is consistent with a more complex *dual-path hypothesis*. According to this hypothesis, temporal orienting and trace conditioning contribute independently to the state of nonspecific preparation.

Los and Van den Heuvel (2001) provided initial evidence for the dual-path hypothesis by showing that cuing effects can be dissociated from sequential effects. They used three equiprobable FPs of 500, 1,000, and 1,500 ms, with a cue specifying the duration of the impending FP with 90% validity. They observed that in the valid-cue condition, sequential effects were strongly reduced as compared with effects in a neutral-cue condition, in which the cue provided no information about the impending FP, again demonstrating the contribution of temporal orienting to nonspecific preparation. However, in the invalid-cue condition, sequential effects were as strong as those in the neutral-cue condition, which was particularly pronounced for the earliest critical moment. That is, sequential effects were observed when the invalid cue had drawn the focus of temporal orienting away from the imperative moment, suggesting that a mechanism other than temporal (re)orienting is

responsible for these effects. Los and Van den Heuvel took this as evidence for the involvement of trace conditioning, which they claimed is the primary cause for sequential effects and the classical FP–RT function. According to this view, temporal orienting may contribute to nonspecific preparation in addition to trace conditioning, but it does not lie at the origin of sequential effects.

Note that the dual-path hypothesis does not impose inherent constraints on how the contributions of trace conditioning and temporal orienting are combined to determine the resulting level of nonspecific preparation. One possibility is that these contributions combine underadditively (e.g., like a logical OR function). Thus, in the study of Los and Van den Heuvel (2001), nonspecific preparation was high as long as the contribution of either temporal orienting or trace conditioning was high. An RT deficit was only observed when both these influences were low, as when FP_n was shorter than FP_{n-1} and an invalid cue specified a critical moment beyond the imperative moment. However, other combinatory rules like additivity or overadditivity may apply for physiological measures, as the present article shows, and perhaps also in other domains of cognitive functioning where dual-path influences apply.

Plan of the Present Study

Building on the Los and Van den Heuvel (2001) study, we used electrophysiological indices to provide more direct evidence for the dual-path hypothesis that both intentional and unintentional influences contribute to nonspecific preparation. We used an experimental design with equiprobable FPs of either 400 or 1,200 ms and a cue that was either neutral, in which case it provided no information about the duration of the impending FP, or informative, in which case it provided valid information about the duration of the impending FP. Note that our factor cuing only comprised a valid and neutral condition but not an invalid condition. Los and Van den Heuvel needed the invalid-cue condition to estimate the level of nonspecific preparation at a critical moment when the influence of intentional orienting was diverted from that moment. In the present study, this estimate was derived covertly from electrophysiological measures, thus making the invalid-cue condition superfluous. Leaving out this condition has the additional advantage of encouraging a stable strategy regarding the use of the cue. This is because participants knew that whenever the cue provided advance information about the impending FP, this information was always valid, so they had no reason not to make use of it. Thus, in the present design, possible contributions of temporal orienting to nonspecific preparation should be maximally traceable.

We used the contingent negative variation (CNV) as a general index of nonspecific preparation and the lateralized readiness potential (LRP) as a more specific index of motor preparation. The CNV is a negative slow wave in the event-related brain potential that develops during the FP, in particular at frontal, central, and parietal scalp locations (e.g., Miniussi, Wilding, Coull, & Nobre, 1999; Rohrbaugh & Gaillard, 1983; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV has a long-standing tradition as a dependent measure in studies of nonspecific preparation, interval timing, and classical or operant conditioning. This research has shown that the CNV may reflect processes of intentional timing (e.g., Macar, Vidal, & Casini, 1999; McAdam, 1966;

Pouthas, Garnero, Ferrandez, & Renault, 2000), conditioning (e.g., Flor et al., 1996; Macar & Vitton, 1979; Walter et al., 1964), anticipation of instruction or feedback (e.g., Brunia & Van Boxtel, 2001), and motor preparation (e.g., Miniussi et al., 1999; Rohrbaugh & Gaillard, 1983). Regarding motor preparation, it is generally believed that the readiness potential (Kornhuber & Deecke, 1965), which is observed just prior to a voluntary response, is part of the later part of the CNV. As a composite signal, the CNV serves the purpose of the present study well because it is likely to reflect the influences of the experimental factors, thus enabling us to examine their combined influence on electrocortical activity.

The LRP (De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988) can be conceived of as the lateralized part of the readiness potential, and its derivation is based on the anatomical fact that hand responses are controlled by the contralateral hemisphere. Thus, as a right-hand response is being prepared, electrodes located over the left motor cortex show a stronger negativity than electrodes located over the right motor cortex do, whereas the reverse is true as a left-hand response is being prepared. By averaging this lateralized activation across left- and right-hand responses, the LRP is obtained. In this procedure, possible hemispheric differences unrelated to the production of the motor response are averaged out, making the LRP a pure measure of motor activation at a central level (for reviews, see Coles, 1989; Eimer, 1998). Because of this quality, the LRP has mainly been used to identify the emergence of motor activation after the presentation of S_2. However, when participants receive advance information about the hand to be used for responding to the impending S_2, an LRP can be observed also during FP (e.g., De Jong et al., 1988; Wijers, Mulder, Okita, Mulder, & Scheffers, 1989). This foreperiod LRP has been shown to be sensitive to advance information about the impending motor response, thus making it a promising measure to examine motor-specific preparation during FP (e.g., Leuthold, Sommer, & Ulrich, 1996; Sangals, Sommer, & Leuthold, 2002).

Regarding the CNV, two predictions were shared by the single-path and dual-path hypotheses. First, we predicted that the asymmetrical sequential effects of FP that are typically observed on RT are also reflected in the amplitude of the CNV. That is, at the early critical moment, we predicted the CNV amplitude to be larger when FP_{n-1} was short than when FP_{n-1} was long, whereas at the late critical moment, we predicted no effect of FP_{n-1}. Second, we predicted an effect of cuing on the CNV at the early critical moment when FP_n is short but no corresponding effect of cuing at the late critical moment when FP_n is long. In the case of a short FP, a valid cue directs temporal orienting to the early critical moment to enhance the participant's preparedness for action, leading to a larger CNV at that moment than when the cue is neutral. By contrast, in the case of a long FP, any uncertainty about the impending imperative moment is resolved as soon as the early critical moment is bypassed, such that participants may confidently orient to the late critical moment even in the neutral-cue condition.

To distinguish between the single-path and dual-path hypotheses, the critical issue is how cuing and FP_{n-1} affect the CNV amplitude in combination rather than in isolation. According to the single-path hypothesis, the effect of FP_{n-1} reflects a strategic use of temporal orienting, driven by uncertainty about the timing of S_2. Therefore, insofar an effect of FP_{n-1} is observed on the CNV, it should be limited to the neutral-cue condition, because in the

valid-cue condition, any uncertainty about the moment of S_2 occurrence is eliminated and with it the basis of sequential effects. By contrast, according to the dual-path hypothesis, the effect of FP_{n-1} reflects an influence of trace conditioning that is independent of the influence of temporal orienting. Therefore, there should be an effect of FP_{n-1} not only in the neutral-cue condition but also in the valid-cue condition. Particularly interesting in this respect is the effect of FP_{n-1} at the early critical moment in the condition where a valid cue specifies a long FP_n. The single-path hypothesis predicts no effect of FP_{n-1} at the early critical moment, because participants orient to the late critical moment. By contrast, the dual-path hypothesis predicts a clear effect of FP_{n-1} at this moment, fully expressing trace conditioning unimpaired by a contribution of temporal orienting.

Finally, we were interested to see to what extent the findings with respect to the CNV, our general index of nonspecific preparation, would generalize to the FP LRP, our specific index of motor preparation. We expected some generalization, because nonspecific preparation is commonly considered to be motoric in nature (e.g., Coull et al., 2000; Rudell & Hu, 2001; Sanders, 1980; Tandonnet, Burle, Vidal, & Hasbroucq, 2003; but see Hackley & Valle Inclán, 2003; Müller-Gethmann, Ulrich, & Rinkenauer, 2003). In fact, Van der Lubbe et al. (2004) observed effects of FP_{n-1} on both the CNV and the LRP, although the latter effect was not very strong and in need of replication.

Experiment 1

In Experiment 1, a cue was presented on each trial, which provided either no information (neutral cue) or valid information (valid cue) about the duration of the impending FP. Participants responded with the same hand to S_2 within each series of six blocks and switched to the other hand between subsequent series. Using this procedure, we expected participants to prepare the responding hand during the S_1–S_2 interval, which should lead to a FP LRP in addition to the CNV (cf. Van der Lubbe et al., 2004; Wijers et al., 1989).

Method

Participants. Twelve undergraduate students (all right handed; five women) participated against a payment of 12.5 Dutch guilders (or €5.68; approximately $7.50) per hour in a single session that lasted about 3.5 hr. Mean age was 22 years, ranging from 19 to 24 years. All participants had normal or corrected-to-normal vision. They reported good general health, and none reported using any prescribed medication at the time of the experiment.

Materials and task. The experiment took place in an electrically shielded, dimly illuminated cubicle. An IBM-compatible personal computer, equipped with a color monitor, controlled the experiment and collected the behavioral data. The software package ERTS was used to program and run the experiment (Beringer, 1992). The computer was connected to a response panel by an interface that allowed measurement of RT to the nearest millisecond. The response panel consisted of four microswitches, which were covered by round response buttons 2.5 cm in diameter. The buttons were spatially arranged from left to right to ensure a comfortable hand position when the index and middle fingers of both hands were rested on top of them.

Participants sat at a distance of about 80 cm from the screen. The stimuli were all white letters or digits (in Helvetica sans serif font, 20-point size) that were presented at the center of the dark screen. The stimuli subtended

0.57 × 0.36° of visual angle. During a block of trials, participants used only one hand for responding. They positioned the middle and index finger of this hand on the response buttons while resting the other hand on the table.

Each trial started with the presentation of a visual cue for 400 ms. The cue was one of the digits *0*, *1*, or *2*. The digit *0* was the neutral cue and provided no information about the duration of the impending FP. The digits *1* and *2* were the informative cues and specified, with 100% validity, impending FPs of 400 ms and 1,200 ms, respectively. The offset of the cue was followed by a FP of 400 or 1,200 ms, after which the imperative stimulus was presented. The imperative stimulus was the capital letter *L* or *R*, which required the participant to press as quickly as possible the left or right response key, respectively. The imperative stimulus disappeared after a response or after a maximum interval of 1,000 ms had expired, whichever occurred earlier. Upon its disappearance, the imperative stimulus was immediately replaced by a feedback message for 200 ms. In the case of a correct response, with an RT below 600 ms, the Dutch word *goed* (good) was presented on the screen. In the case of an incorrect response, with an RT below 1,000 ms, the Dutch word *fout* (wrong) was presented. In the case of a correct response with an RT greater than 600 ms or a failure to respond within 1,000 ms, the Dutch word *traag* (slow) was presented. (The upper time limit of 600 ms was used only during the experimental sessions to emphasize fast responding; in the data analysis, RTs up until 800 ms were accepted.) The next trial started after an intertrial interval of 1,500 ms.

Electrophysiological recordings. Electroencephalographic (EEG) data were recorded continuously from standard scalp locations Fz, Cz, C3, and C4, as well as from the left mastoid, all referred to the right mastoid (Nuwer et al., 1998).[2] The left cheek was grounded. Horizontal electrooculogram (EOG) was recorded between the outer canthi of each eye, vertical EOG from above and below the right eye. The scalp electrodes were mounted in an elastic cap; the skin electrodes were attached individually by means of double-sided adhesive rings. Impedances were kept below 5 kΩ. All electrodes were made of sintered Ag/AgCl material (Electrocap International, Eaton, OH). All electrophysiological data were DC amplified, low-pass filtered (bandwidth 0–70 Hz), digitized (500 Hz, 16 bits), and stored on computer disk using Neuroscan (Sterling, VA) amplifiers and software.

Design and procedure. The design was a three-factorial within-subjects design, with FP_n (400 or 1,200 ms), FP_{n-1} (400 or 1,200 ms), and cuing (valid or neutral) as independent variables. Both FP_n and FP_{n-1} were varied within blocks of trials. Cuing was alternated between subsequent blocks of trials. Responding hand (right or left) was alternated after each sixth block of trials. The order of cuing and responding hand was counterbalanced over participants.

Each participant completed an experimental session individually. After the experimenter attached the electrodes, the participant practiced the task in four blocks of 20 trials involving each combination of responding hand (left or right) and cue (valid or neutral). After each block, participants were told to respond faster if their average RT exceeded 400 ms, to respond more accurately if their percentage of errors exceeded 5%, and, in the case of eyeblinks causing artifacts in the EEG, to postpone blinking until after their response. Then participants completed 48 blocks of 36 trials each, scheduled in eight series of 6 blocks. Each new series of 6 blocks was preceded by a short 12-trial practice block that served to remind the participant of the stimulus–response mapping of the relevant responding hand. After each block, participants could initiate the next block whenever they felt ready. After each series of 6 blocks, participants received feedback on their performance, in the same way as during practice. After each second series (i.e., 12 blocks), participants were allowed to take a 10-min break outside the cubicle.

Data analysis. Electrophysiological data were digitally low-pass filtered (bandwidth 0–40 Hz, without phase lags) and cut in epochs of 1,550-ms duration for trials with a short FP_n and 2,350-ms duration for trials with a long FP_n. In both cases, the first 250 ms preceded the

presentation of the cue and served as prestimulus baseline. Trials with erroneous manual responses, reaction times shorter than 150 ms or longer than 800 ms, or artifacts in any EEG or EOG channel were omitted from further analyses. The artifact criterion was an amplitude range not larger than ±65 µV during the first 1,350 ms for short FP_n trials and not larger than ±75 µV during the first 2,150 ms for long FP_n trials.[3] Of all trials on which responding was correct, 6.1% were discarded because artifact criteria were exceeded. This percentage was somewhat lower for the trials with a short FP_{n-1} (4.9%) than for the trials with a long FP_{n-1} (7.3%), suggesting that some strain of delayed blinking carried over from one trial to the next. The EEG data stemming from correct and artifact-free trials were averaged separately according to FP_n, FP_{n-1}, and cuing and were rereferenced to the mean between both mastoids. For each participant and condition, the CNV was quantified at the frontocentral scalp locations Fz and Cz as the mean amplitude over consecutive time windows of 200-ms width (four windows for short FP_n trials, eight windows for long FP_n trials), the first starting 100 ms after the onset of the cue. The LRP was derived by averaging the differences obtained by subtracting electrode C4 from C3 for right-hand responses and C3 from C4 for left-hand responses (cf. Coles, 1989). The resulting LRP was quantified in the same way as the CNV.

Results

Behavioral data. Figure 1 shows mean RTs and mean error percentages as a function of FP_n, FP_{n-1}, and cuing. Table 1 presents a summary of the results of an analysis of variance (ANOVA) of these data, with FP_n, FP_{n-1}, and cuing as within-subjects factors. We analyzed the significant three-way interaction among all factors in detail by testing simple (interaction) contrasts. As Figure 1 suggests, the interaction between FP_{n-1} and cuing was highly significant for the short FP_n, $F(1, 11) = 24.53$, $MSE = 15.02$, $p < .001$, $\eta_p^2 = .69$, but not for the long FP_n, $F < 1$. The significant interaction between FP_{n-1} and cuing for the short FP_n was due to the fact that the effect of FP_{n-1} was much larger in the neutral-cue condition (17 ms), $F(1, 11) = 90.40$, $MSE = 19.18$, $p < .001$, $\eta_p^2 = .89$, than in the valid-cue condition (7 ms), $F(1, 11) = 5.90$, $MSE = 35.59$, $p < .05$, $\eta_p^2 = .35$.

We arcsine transformed the error proportions to stabilize the variances across conditions (cf. Winer, Brown, & Michels, 1991). The ANOVA of the resulting data, with FP_n, FP_{n-1}, and cuing as within-subjects factors, yielded significant main effects of FP_n, $F(1, 11) = 9.01$, $MSE = 0.009$, $p < .05$, $\eta_p^2 = .45$, and of cuing, $F(1, 11) = 10.00$, $MSE = 0.007$, $p < .01$, $\eta_p^2 = .48$, as well as a significant interaction between these variables, $F(1, 11) = 7.81$, $MSE = 0.007$, $p < .05$, $\eta_p^2 = .42$. The interaction indicates a higher error percentage in the valid-cue condition (4.03%) than in the neutral-cue condition (2.22%) when FP_n was short, $F(1, 11) = 11.78$, $MSE = 0.010$, $p < .01$, $\eta_p^2 = .52$, whereas this difference was not significant when FP_n was long, $F < 1$.

CNV. In a first analysis of the ERP waveforms, we examined the development of the CNV during FP up until and including the first critical moment as a function of FP_n, FP_{n-1}, and cuing. Figure 2 shows these waveforms for the Fz and Cz electrodes. These waveforms were analyzed in four consecutive 200-ms time win-

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[2] For purposes beyond this study, we also recorded from the scalp locations Pz, Oz, F3, P3, T5, F4, P4, and T6.

[3] Data from the last 200 ms of each epoch were not screened for artifacts, because they were beyond the preparation interval of present interest, and not analyzed statistically.
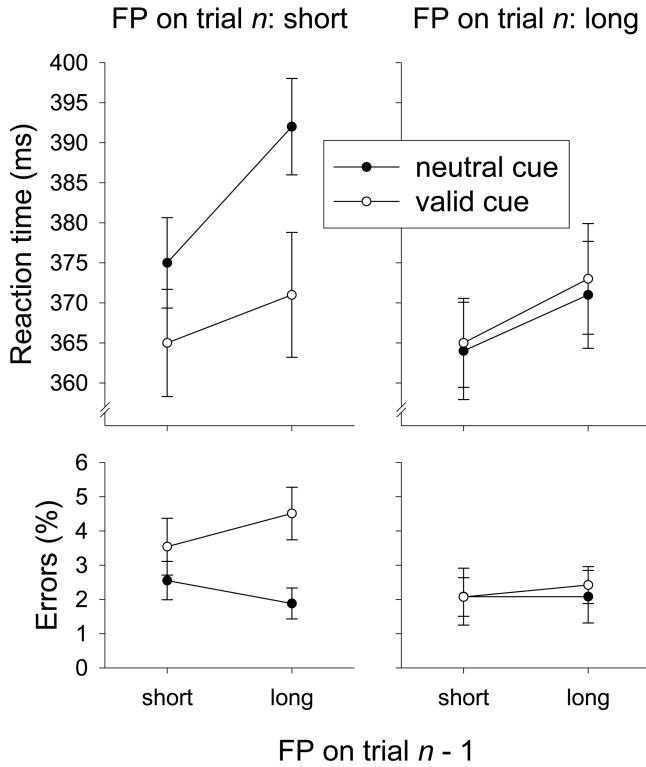
FP on trial *n*: short   FP on trial *n*: long

neutral cue
valid cue

FP on trial *n* - 1

Figure 1. Mean reaction times and mean error percentages in Experiment 1 as a function of the foreperiod (FP) on trial *n* (from which reaction time was sampled), the FP on trial *n* − 1, and cuing. Error bars represent standard errors of the mean.

dows, running from 100 ms to 900 ms after the onset of S_1. Note that in the case of a short FP_n, S_2 occurred in the middle of the last time window (700–900 ms) and evoked an ERP from about 950 ms onward. Consequently, whether or not S_2 was presented did not affect the CNV in the last time window, as indicated by the fact that in the neutral-cue condition, the waveforms for the short FP_n overlapped the corresponding waveforms for the long FP_n throughout this window.

Separate ANOVAs were conducted on the mean amplitudes obtained in each time window as a function of FP_n, FP_{n-1}, and cuing. A summary of the significant results is presented in Table

2. Note that the increasing effect of FP_{n-1} across time windows at both Fz and Cz indicates that in approaching and bypassing the earliest critical moment, the CNV was larger (more negative) when FP_{n-1} was short than when it was long. Cuing had also a clear main effect on the waveforms during the S_1–S_2 interval, but it had a time profile that differed from that of FP_{n-1}. At Fz, cuing had both an early and a late effect, but it had no effect in intermediate time windows (i.e., it had no effect in the second and third window); at Cz, the effect of cuing was limited to the first two time windows. In none of the time windows was there a significant interaction between FP_{n-1} and cuing, largest $F(1, 11) = 1.91$, $MSE = 0.54$, $p = .19$.

Both the early and the late effects of cuing were modified by FP_n. The early modification in the first time window reflects a greater positivity in the valid-cue condition than in the neutral-cue condition, in particular when the cue specified the early critical moment. Tests for simple effects confirmed that at both Fz and Cz, the positivity in the first time window was greater when the valid cue specified the short FP than when it specified the long FP, $F(1, 11) = 5.79$, $MSE = 1.14$, $p < .05$, $\eta_p^2 = .34$, for Fz, and $F(1, 11) = 12.12$, $MSE = 0.83$, $p < .01$, $\eta_p^2 = .52$, for Cz. Further, it was also greater in the valid-cue condition specifying the long FP than in the neutral-cue condition, $F(1, 11) = 13.95$, $MSE = 0.55$, $p < .01$, $\eta_p^2 = .56$, for Fz, and $F(1, 11) = 13.68$, $MSE = 0.54$, $p < .01$, $\eta_p^2 = .55$, for Cz.

Regarding the late modification of the waveforms in the fourth time window, the interaction between cuing and FP_n indicates that there was no effect of cuing when FP_n was long, $F(1, 11) < 1$ for Fz, and $F(1, 11) = 2.00$, $MSE = 2.46$, $p = .19$, $\eta_p^2 = .15$, for Cz. However, the effect of cuing was highly significant when FP_n was short, $F(1, 11) = 18.52$, $MSE = 3.12$, $p < .01$, $\eta_p^2 = .63$, for Fz, and $F(1, 11) = 16.01$, $MSE = 2.22$, $p < .01$, $\eta_p^2 = .59$, for Cz. Thus, in the case of a long FP_n, the only variable that affected the waveform in the time window surrounding the first critical moment was FP_{n-1}. In the case of a short FP_n, an independent additional contribution to this waveform was delivered by cuing.

In a second analysis, we examined the development of the CNV during FP up until and including the second critical moment for those trials on which FP_n was long as a function of cuing and FP_{n-1}. Figure 3 shows these waveforms for the Fz and Cz electrodes. Separate ANOVAs were conducted on the average amplitude in each of eight 200-ms time windows, from 100 ms to 1,700 ms relative to the onset of S_1, with cuing and FP_{n-1} as within-

Table 1
Summary of the Analyses of Variance of Reaction Times in Experiments 1 and 2

	Experiment 1			Experiment 2		
Source	η_p^2	*MSE*	*F*(1, 11)	η_p^2	*MSE*	*F*(1, 15)
Foreperiod on trial *n* (FP_n)	.49	123.17	10.48**	.01	123.98	0.16
Foreperiod on trial *n* − 1 (FP_{n-1})	.75	61.21	32.95**	.42	37.17	10.93**
Cuing	.36	178.32	6.13*	.36	108.78	8.50*
$FP_n \times FP_{n-1}$	.43	15.18	8.30*	.20	55.92	3.67
$FP_n \times$ Cuing	.49	162.81	10.76**	.53	81.82	16.68**
$FP_{n-1} \times$ Cuing	.32	28.41	5.11*	.52	20.18	16.12**
$FP_n \times FP_{n-1} \times$ Cuing	.76	6.49	35.19**	.38	20.23	9.16**

* $p < .05$.   ** $p < .01$.

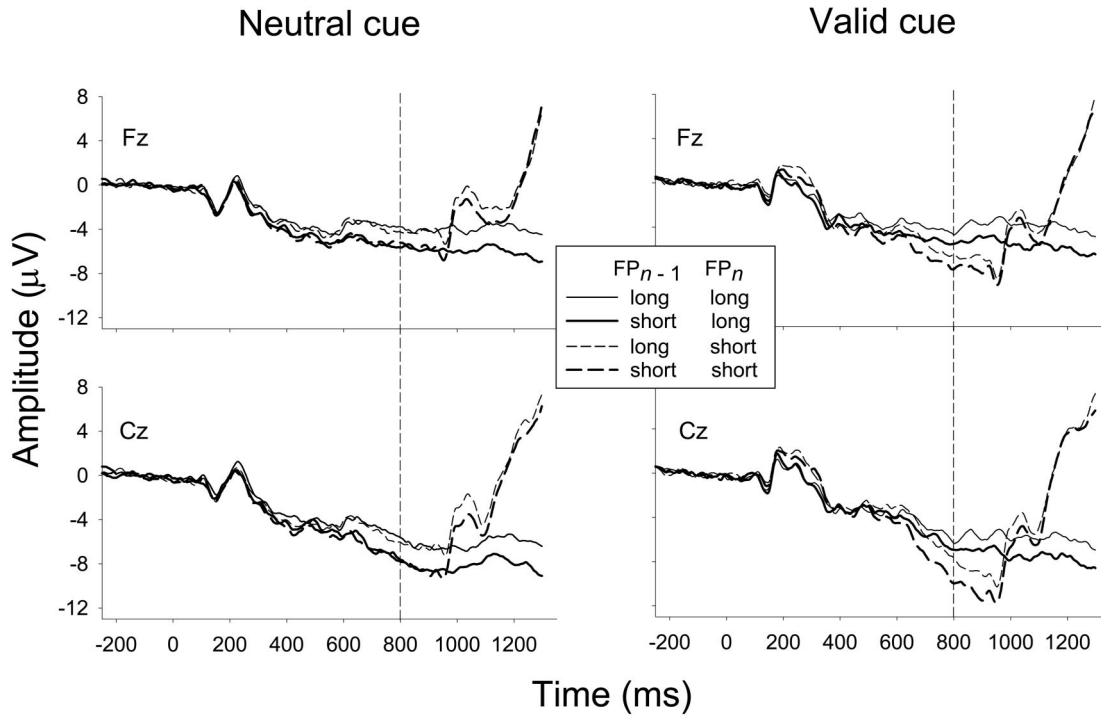## Neutral cue   Valid cue

Figure 2. Mean waveforms at frontal (Fz) and central (Cz) scalp locations in Experiment 1 up until and including the first critical moment (indicated by the broken vertical line) as a function of the foreperiod on trial n (FP$_n$) and the foreperiod on trial $n - 1$ (FP$_{n-1}$), separately for neutral and valid cues.

subjects factors. A summary of the significant results of these ANOVAs is presented in Table 3. Note that there was an early main effect of cuing that was limited to the first time window for Fz and to the first two time windows for Cz. Consistent with the analysis reported above, this effect indicates a greater early positivity when the cue validly specified the late critical moment than when the cue was neutral. The effect of FP$_{n-1}$ started somewhat later, in the second time window for Fz and in the third time window for Cz, and remained highly significant throughout the entire waveform up to S$_2$. Also note that there was again no significant interaction between cuing and FP$_{n-1}$ throughout the entire S$_1$–S$_2$ interval, although this interaction effect approached significance in the fourth time window at Cz, $F(1, 11) = 4.80$, $MSE = 0.83$, $p = .051$, $\eta_p^2 = .30$, but not at Fz, $F(1, 11) = 1.32$, $MSE = 1.53$, $p = .27$.

Finally, in the valid-cue condition with a long FP$_n$ (i.e., when participants knew that the impending FP would be long), planned comparison between the CNV amplitudes of the short and long FP$_{n-1}$ in the fourth time window yielded a significant effect at both Fz, $F(1, 11) = 9.15$, $MSE = 0.93$, $p < .01$, $\eta_p^2 = .45$, and Cz, $F(1, 11) = 4.54$, $MSE = 1.28$, $p < .05$, $\eta_p^2 = .29$ (both tests one sided). As can be seen in both Figure 2 (right panels) and Figure 3, the CNV for the validly cued long FP$_n$ (solid lines) attained a more negative value in the fourth time window when FP$_{n-1}$ was short (-5.25 μV at Fz and -6.51 μV at Cz) than when FP$_{n-1}$ was long (-4.07 μV at Fz and -5.53 μV at Cz).

LRP. Figure 4 shows the LRP waveforms as a function of FP$_n$, FP$_{n-1}$, and cuing. Surprisingly, the LRP showed a positive deflection from zero throughout the S$_1$–S$_2$ interval instead of the ex-

pected negative deflection. Separate ANOVAs run on each of the first four time windows and including FP$_n$, FP$_{n-1}$, and cuing as within-subjects factors revealed that this positive deflection was significant in all time windows, smallest $F(1, 11) = 8.34$, $MSE = 2.00$, $p < .05$, $\eta_p^2 = .43$. These ANOVAs also yielded a significant main effect of FP$_{n-1}$ in the first time window, $F(1, 11) = 37.64$, $MSE = 0.02$, $p < .01$, $\eta_p^2 = .77$, and the third time window, $F(1, 11) = 5.51$, $MSE = 0.19$, $p < .05$, $\eta_p^2 = .33$, whereas this effect was a trend in the second time window, $F(1, 11) = 3.45$, $MSE = 0.13$, $p = .09$, $\eta_p^2 = .24$. In all cases, the LRP was more negative when FP$_{n-1}$ was long than when FP$_{n-1}$ was short. The ANOVAs yielded no other significant effects, largest $F(1, 11) = 2.90$, $MSE = 0.15$, $p = .12$.

Separate ANOVAs on each of the eight time windows for the long FP$_n$, with cuing and FP$_{n-1}$ as factors (see Figure 4, bottom panel), revealed that the positive deflection of the LRP from 0 was significant up until the sixth time window, smallest $F(1, 11) = 5.18$, $MSE = 1.29$, $p < .05$, $\eta_p^2 = .32$, and dropped below significance thereafter. The effect of FP$_{n-1}$ was again significant in the first time window, $F(1, 11) = 4.88$, $MSE = 0.10$, $p < .05$, $\eta_p^2 = .31$, and approached significance in the third time window, $F(1, 11) = 4.77$, $MSE = 0.49$, $p = .052$, $\eta_p^2 = .30$, in both cases indicating a more negative LRP when FP$_{n-1}$ was long than when FP$_{n-1}$ was short. The ANOVAs yielded no other significant effects, largest $F(1, 11) = 2.53$, $MSE = 0.29$, $p = .14$.

Electrophysiological–behavioral correspondence. Finally, we examined the relation between behavior, as indexed by RT, and nonspecific preparation, as indexed by the CNV amplitude. Across participants and separately for each of the eight experimental

Table 2

Summary of Significant Effects in the Analyses of Variance of the Event-Related Potentials at Frontal (Fz) and Central (Cz) Scalp Sites in Experiment 1 Within Four 200-ms Time Windows, With Foreperiod on Trial n (FP_n), Foreperiod on Trial n − 1 (FP_{n-1}), and Cuing as Factors

Source	Time window (s)			
	0.1–0.3	0.3–0.5	0.5–0.7	0.7–0.9
Fz				
FP_n				
η_p^2				.52
MSE				2.61
$F(1, 11)$				12.06
FP_{n-1}				
η_p^2		.47	.69	.82
MSE		0.65	1.07	0.81
$F(1, 11)$		9.60*	24.82**	48.80**
Cuing				
η_p^2	.75			.52
MSE	1.00			0.28
$F(1, 11)$	33.13**			11.83**
$FP_n \times FP_{n-1}$				
η_p^2				
MSE				
$F(1, 11)$				
$FP_n \times$ Cuing				
η_p^2	.33			.04
MSE	0.75			1.59
$F(1, 11)$	5.50*			19.59**
$FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
$F(1, 11)$				
$FP_n \times FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
$F(1, 11)$				
Cz				
FP_n				
η_p^2	.39			.69
MSE	0.42			1.70
$F(1, 11)$	6.89*			24.90**
FP_{n-1}				
η_p^2			.68	.81
MSE			0.97	1.39
$F(1, 11)$			23.22**	46.51**
Cuing				
η_p^2	.71	.55		
MSE	1.41	2.87		
$F(1, 11)$	26.28**	13.27**		
$FP_n \times FP_{n-1}$				
partial η_p^2				
MSE				
$F(1, 11)$				
$FP_n \times$ Cuing				
η_p^2	.53	.34		.64
MSE	0.62	0.54		1.68
$F(1, 11)$	12.47**	5.61*		19.90**
$FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
$F(1, 11)$				
$FP_n \times FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
$F(1, 11)$				

* $p < .05$.   ** $p < .01$.

conditions, we calculated mean RT and the corresponding mean CNV, averaged across a 200-ms time window surrounding the imperative moment. The Pearson product–moment correlation between these variables was .89 at Fz, $F(1, 6) = 26.01$, $MSE = 17.93$, $p < .01$, adjusted $R^2 = .78$, and .82 at Cz, $F(1, 6) = 13.48$, $MSE = 29.47$, $p < .05$, adjusted $R^2 = .64$. After we applied a log transform to the CNV amplitudes (see Figure 5), the correlation coefficient increased to .94 at Fz (adjusted $R^2 = .88$) and to .87 at Cz (adjusted $R^2 = .72$). This increase was significant by Williams's statistic (Steiger, 1980) both at Fz, $T_2(5) = 4.49$, $p < .01$, and at Cz, $T_2(5) = 2.36$, $p < .05$ (one sided).

Discussion

The RT data of Experiment 1 replicated those of earlier studies. First, we observed asymmetric sequential effects of FP in the neutral-cue condition (see also, e.g., Karlin, 1959; Los et al., 2001; Van der Lubbe et al., 2004; Woodrow, 1914; Zahn et al., 1963). For the short FP_n, RT was longer when FP_{n-1} was long than when it was short. This sequential effect was strongly reduced for the long FP_n, although it was not quite eliminated, as is more commonly observed in this condition (e.g., Granjon & Reynard, 1977; Los & Van den Heuvel, 2001; Los et al., 2001; Possamaï, Granjon, Reynard, & Requin, 1975). Second, as compared with the neutral-cue condition, a strong reduction of the sequential effect was observed in the valid-cue condition for the short FP_n but not for the long FP_n (see also Los & Van den Heuvel, 2001). As a result, the FP–RT function was about flat in the valid-cue condition, consistent with the findings in a number of earlier studies (e.g., Coull et al., 2000; Kingstone, 1992, Experiment 4; Los & Van den Heuvel, 2001; Mo & Kersey, 1980; Nobre, 2001; Zahn, 1970). Together, these findings indicate that participants were capable of using the symbolic information of the cue to orient to the specified critical moment so as to enhance their state of preparedness for action at that moment. The efficacy of this strategy was limited to those conditions where the initial state of preparation was low, in particular when FP_{n-1} was longer than FP_n.

When considered isolated from the electrophysiological data, these findings can be interpreted in either of two ways. According to the single-path hypothesis, they could be taken to indicate that in the neutral-cue condition, participants initially orient to the critical moment that was the imperative moment on the last trial. When this focus turns out to be false, there is still time during FP to reorient from the early to the late critical moment but not vice versa (cf. Niemi & Näätänen, 1981; Requin et al., 1991), thus leading to asymmetric sequential effects. In the valid-cue condition, explicit cuing replaces the implicit cuing by FP_{n-1}, thereby optimizing the selected moment for temporal orienting and reducing sequential effects for the short FP_n. In contrast, according to the dual-path hypothesis, the preceding FP contributes unintentionally to the state of nonspecific preparation by the process of trace conditioning, while a valid cue may bring an additional influence of intentional orienting to bear on the state of nonspecific preparation at the specified critical moment. If these influences of trace conditioning and temporal orienting combine underadditively (e.g., like a logical OR function), the observed RT data are readily explained (Los & Van den Heuvel, 2001).

Strong support for the dual-path architecture derives from the observed event-related brain potentials. The effects of cuing and
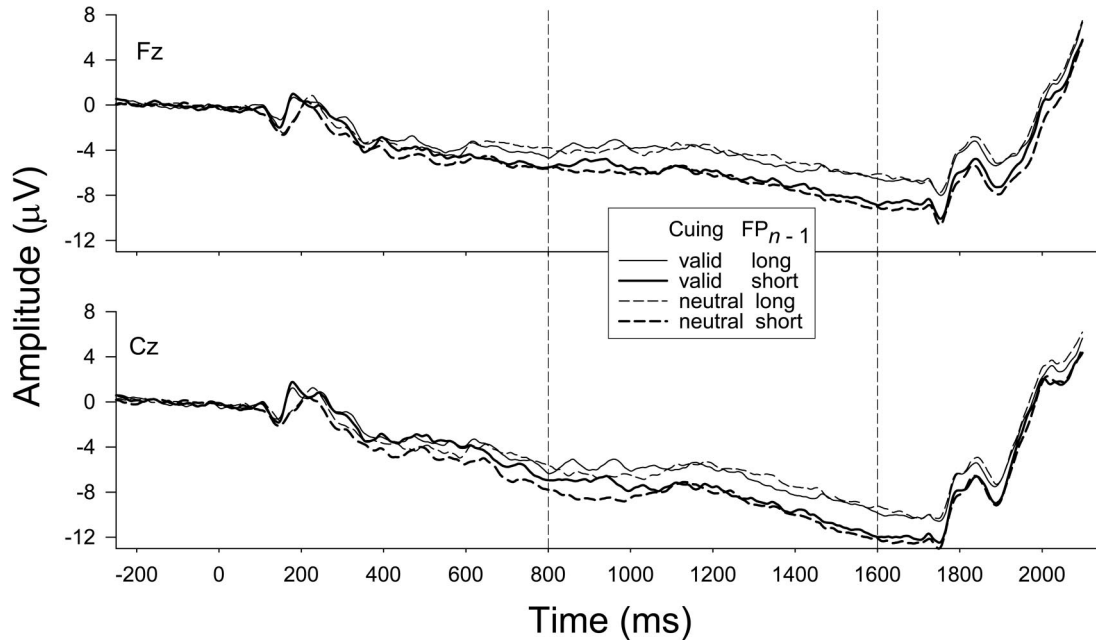
Figure 3. Mean waveforms at frontal (Fz) and central (Cz) scalp locations in Experiment 1 up until and including the second critical moment as a function of the foreperiod on trial $n - 1$ (FP_{n-1}) and cuing. Vertical broken lines correspond to the critical moments; only the conditions with a long foreperiod on trial n are shown.

FP_{n-1} on the CNV amplitude were approximately additive throughout the entire S_1–S_2 interval. In some time windows, this additivity may be attributable to insufficient statistical power, as suggested by the fact that the Cuing $\times$ FP_{n-1} interaction approached significance in the fourth time window at Cz. But even so, the more important finding is that preknowledge about the impending FP did not erase the effect of FP_{n-1} either at Fz or at Cz. The most compelling observation in this respect was that of an effect of FP_{n-1} in the fourth time window (which surrounds the early critical moment) in the condition where a valid cue specified a long FP. Despite the fact that participants knew that the impending FP would be long and thus were discouraged from making any intentional contribution to the state of preparation at the early critical moment, the CNV in the fourth time window was larger when FP_{n-1} was short than when it was long. This finding indicates that FP_{n-1} influenced nonspecific preparation through a process other than cuing. It is interesting to note that a similar persistence of the effect of FP_{n-1} in the fourth time window was observed when FP_n was short. In this case, the effects of cuing and FP_{n-1} were both fully developed by this time, yet the interaction between these variables was far from significant. This finding strongly suggests that the contributions of cuing and FP_{n-1} stem from different sources, whose influences combine additively at the cortical level (e.g., Heslenfeld, Kenemans, Kok, & Molenaar, 1997; Kounios, 1996; Sternberg, 2001).

The complete ERP time series revealed additional evidence for separate intentional and unintentional contributions to nonspecific preparation. Starting from the onset of S_1, cuing affected some early ERP components, beginning with the frontocentral N1/P2 component (for similar early effects, see, e.g., Backs & Grings, 1985; Flor et al., 1996), whereas FP_{n-1} did not. This early effect of cuing disappeared after the first time window at Fz and after the second time window at Cz, indicating that it should be distinguished from the effect on the CNV amplitude occurring later on. Next, there was an effect on the CNV amplitude of both cuing and FP_{n-1} in close temporal proximity of the first critical moment. However, the effect of FP_{n-1} started earlier (somewhere around 500 ms after the onset of S_1) than the effect of cuing did (not before 600 ms). In addition, the effect of cuing was completely dependent on FP_n, reflecting the efforts of participants to be prepared to respond at the early critical moment if it was specified by the cue, whereas the effect of FP_{n-1} was independent of FP_n. In fact, whereas the effect of cuing was limited to the short FP_n condition, the effect of FP_{n-1} was tonic and continued throughout the long FP_n. The absence of an effect of cuing at the late critical moment in the long FP_n condition may reflect that the event of bypassing the early critical moment resolves any uncertainty about the timing of S_2, after which participants may confidently orient to the late critical moment even in the neutral condition. The unreduced effect of FP_{n-1} at the late critical moment was not predicted but constitutes a remarkable contrast with the absence of an effect of cuing in this time window, thus adding to the evidence for the dual-path hypothesis.

A final noteworthy difference between the effects of cuing and of FP_{n-1} concerns the findings with respect to the error rates. We found that whenever RT was reduced in the valid-cue condition relative to the neutral-cue condition, this was offset by an increase in the error rate. A similar shift in speed–accuracy trade-off was much less pronounced and statistically nonsignificant for RT variations brought about by the sequential order of FPs. This dissociation is difficult to explain when it is assumed that effects of cuing and FP_{n-1} are expressions of a similar intentional process. By

Table 3

Summary of Significant Effects in the Analyses of Variance of the Event-Related Potentials at Frontal (Fz) and Central (Cz) Scalp Sites in Experiment 1 Within Eight 200-ms Time Windows, With Foreperiod on Trial n − 1 (FP_{n-1}) and Cuing as Factors

	Time window (s)							
Source	0.1–0.3	0.3–0.5	0.5–0.7	0.7–0.9	0.9–1.1	1.1–1.3	1.3–1.5	1.5–1.7
				Fz				
FP_{n-1}								
η_p^2		.46	.62	.81	.88	.91	.82	.75
MSE		0.56	0.66	0.55	0.49	0.49	1.10	2.16
$F(1, 11)$		9.38*	17.76**	47.47**	84.00**	104.74**	48.60**	32.21**
Cuing								
η_p^2	.54							
MSE	0.54							
$F(1, 11)$	12.85**							
$FP_{n-1} \times$ Cuing								
η_p^2								
MSE								
$F(1, 11)$								
				Cz				
FP_{n-1}								
η_p^2			.39	.72	.84	.76	.72	.79
MSE			0.71	1.04	0.64	1.31	2.00	1.67
$F(1, 11)$			7.02*	27.87**	56.64**	35.00**	28.43**	41.12**
Cuing								
η_p^2	.46	.34						
MSE	0.60	1.72						
$F(1, 11)$	9.19*	5.69*						
$FP_{n-1} \times$ Cuing								
η_p^2								
MSE								
$F(1, 11)$								

* $p < .05$. ** $p < .01$.

contrast, from the perspective of the dual-path hypothesis, this finding can be readily accommodated by assuming that the unintentional preparatory mechanism, through which FP_{n-1} affects behavior, is better tuned to the impending task demands than the intentional preparatory mechanism, through which cuing affects behavior.

Whereas these findings provide strong support for the dual-path hypothesis, they argue against our proposal that the influences of trace conditioning and temporal orienting combine underadditively (e.g., like a logical OR function) to determine the level of nonspecific preparation. In fact, we observed roughly additive effects of cuing and FP_{n-1} on nonspecific preparation, as indexed by the CNV amplitude, which raises the question of how the strong interaction of these factors on the behavioral level, as indexed by RT, comes about. One possible solution is to assume that the expression of nonspecific preparation in behavior is subject to diminishing returns, implying that one additional unit of preparation leads to a greater RT reduction if the initial state of preparation is low rather than high. This assumption is supported by our finding that the correlation between the CNV amplitude at the imperative moment and the corresponding RT was higher when the CNV values were presented on a logarithmic scale than when they were presented on a linear scale.

Finally, the LRP findings deviated from our expectations. The hallmark of the LRP is a negative deflection during the preparation and execution of a hand response, but we observed a positive deflection throughout the FP. Furthermore, in contrast with recent findings by Van der Lubbe et al. (2004), we observed in some early time windows a more positive LRP amplitude when FP_{n-1} was short than when FP_{n-1} was long, suggesting that the state of motor preparation was lower in the former case. These positive deflections may reflect an inhibition of the responding hand to avoid premature responding during the FP, which may show up when the responding hand is varied between blocks of trials. Using this between-blocks manipulation, we implemented an easy task that enabled participants to maximize temporal orienting in the case of a valid cue. However, an apparent drawback of this procedure is that it may have reduced the need for preparation of the responding hand on each single trial, which may be a necessary condition to elicit the common, negative-going LRP. Therefore, in Experiment 2, we varied the responding hand on a trial-by-trial basis. In the General Discussion, we return to the LRP findings of Experiment 1.

Experiment 2

In Experiment 2, we required participants to choose between a left-hand and a right-hand response on a trial-by-trial basis, to create better conditions than those in Experiment 1 for observing the common negative-going LRP during FP. We implemented this
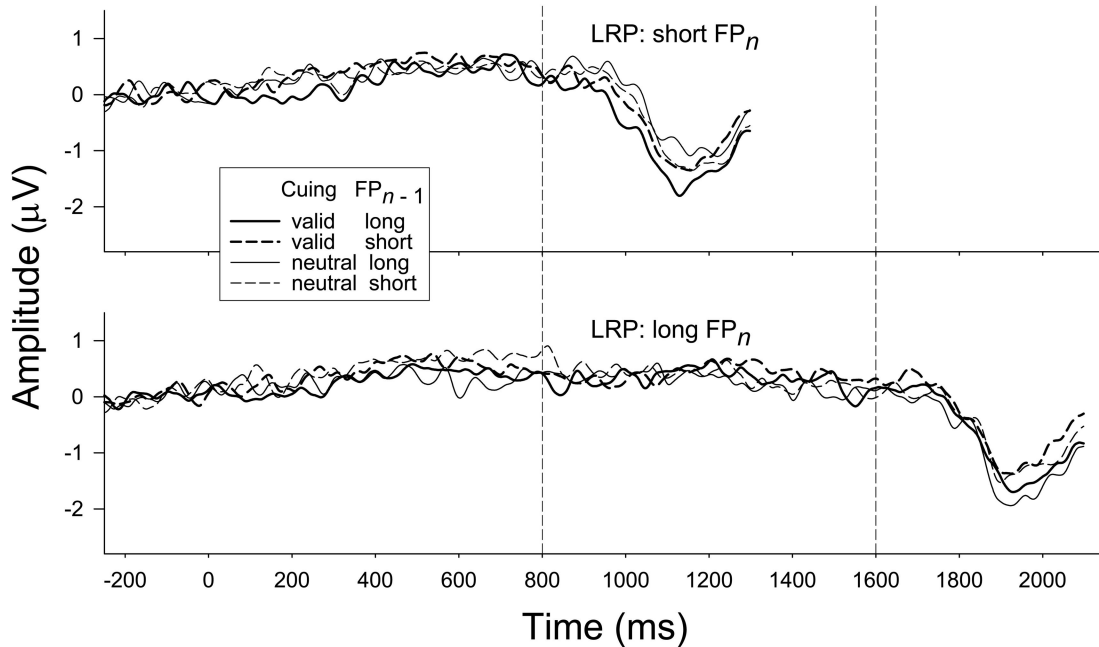
Figure 4. Mean lateralized readiness potential (LRP) waveforms in Experiment 1 as a function of the foreperiod on trial n (FP$_n$), the foreperiod on trial $n - 1$ (FP$_{n-1}$), and cuing. Vertical broken lines correspond to the critical moments.

procedure by prefixing an 800-ms episode to each trial of Experiment 1 during which the color of a fixation cross specified whether a left-hand or right-hand response was required to the impending S$_2$. Using a similar procedure, Leuthold et al. (1996) observed a pronounced negative LRP, which proved sensitive to the specificity of motor preparation, as induced by a cue that was an integral part of S$_1$. On the basis of this finding, we expected to

observe a negative LRP of sufficient magnitude to reflect possible modifications of FP$_{n-1}$ and cuing.

Method

Participants. Sixteen students (14 right handed; 10 women) participated in a 1-hr practice session and a 4-hr experimental session, which were scheduled on separate days. The participants' mean age was 22 years, ranging from 18–28 years. All participants had normal or corrected-to-normal vision. They reported good general health, and none reported using any prescribed medication at the time of the experiment. They received €7 (approximately $9.25) per hour. None of them had participated in Experiment 1.

Materials and task. The apparatus was the same as that used in Experiment 1. Throughout the experiment, participants positioned the middle and index fingers of both hands on the response buttons. Each trial started with a 800-ms presentation of S$_0$, a red or green plus symbol at the center of the screen. S$_0$ subtended about $1 \times 1°$ of visual angle given a viewing distance of 80 cm. For half of the participants, a red plus indicated that a left-hand response to the impending S$_2$ was required, whereas a green plus indicated that a right-hand response was required. For the other half of the participants, this assignment was reversed. After S$_0$ disappeared, S$_1$ (i.e., the digit *0* in blocks with neutral cues and the digit *1* or *2* in blocks with valid cues) appeared onscreen immediately. After this, the sequence of events was identical to that of Experiment 1, with the exception that, instead of a letter *L* or *R*, S$_2$ was a $<$ or $>$ symbol (in Helvetica sans serif font, 20-point size) that specified the middle and index fingers, respectively, for left-hand responses and the index and middle fingers, respectively, for right-hand responses. The intertrial interval was 1,600 ms.

Electrophysiological recordings. The electrophysiological recordings were the same as in Experiment 1. In addition, we recorded the electromyogram (EMG) bipolarly on each forearm just over the finger flexors. This measurement served to identify trials on which participants moved, by
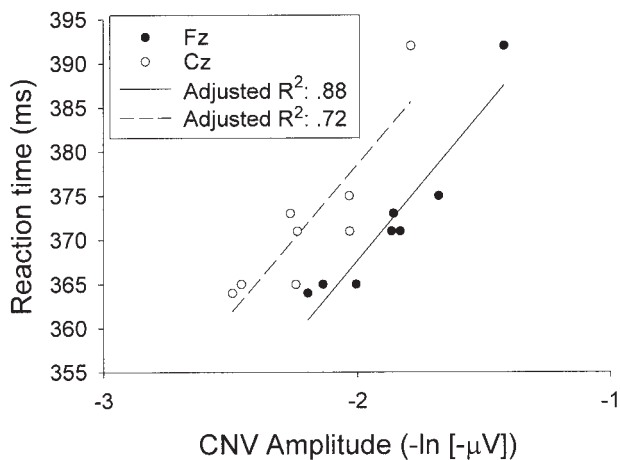

Figure 5. The relation between mean reaction time for the eight experimental conditions and the logarithmically transformed contingent negative variation (CNV) amplitude averaged across the 200-ms interval around the corresponding imperative moment in Experiment 1. Fz = frontal scalp location; Cz = central scalp location.

way of preparation during FP, the fingers of the hand specified by S_0. We discarded these trials, because they would reveal an LRP elicited by overt motor activation instead of central preparatory activation. The EMG was band-pass filtered online (20–200 Hz), and the digitization rate of all channels was increased to 1,000 Hz.

Design and procedure. The design was the same as that in Experiment 1, except the responding hand had to be chosen on each trial instead of being alternated after each series of six blocks. Because this design imposed a higher processing load on the participant than the design of Experiment 1 did, each participant completed a 1-hr practice session without the measurement of brain potentials prior to the experimental session. At the start of the experimental session, each participant completed a 2-min heterochromatic flicker-fusion procedure that equated the subjective luminance of the red and green color of the plus symbol. Next, they completed two 40-trial practice blocks, one with the neutral cue and one with the valid cue, followed by 42 experimental blocks of 40 trials each, scheduled in seven series of 6 blocks. In all other respects, the procedure of Experiment 1 was followed.

Date analysis. Consistent with Experiment 1, we used the first 250 ms preceding S_1 as a baseline, thereby abstaining from an analysis of possible effects on the CNV and LRP occurring in the S_0–S_1 interval. This choice was motivated by two considerations: first, to remain focused on the purpose of this study to uncover mechanisms of preparation for moments in time, and second, to allow maximal comparability with the results of Experiment 1.[4] Furthermore, in addition to the criteria used in Experiment 1 to discard data from individual trials, we excluded trials on which signal amplitude exceeded 200 μV in the rectified and then low-pass filtered ($<$ 40 Hz) EMG. Of all trials on which responding was correct, 13.3% were discarded because artifact criteria were exceeded. This percentage was somewhat higher than in Experiment 1 because of the additional EMG criterion and the longer trial duration. Like in Experiment 1, this percentage was slightly lower for the trials with a short FP_{n-1} (12.4%) than for the trials with a long FP_{n-1} (14.3%).

Results

Behavioral data. Figure 6 shows mean RTs and mean error percentages as a function of FP_n, FP_{n-1}, and cuing. Table 1 presents a summary of the results of the ANOVA of these data, with FP_n, FP_{n-1}, and cuing as within-subjects factors. Concerning RT, the findings were in close agreement with those of Experiment 1. We analyzed the significant three-way interaction among all factors in detail by testing simple (interaction) contrasts. As Figure 6 suggests, the interaction between FP_{n-1} and cuing was highly significant for the short FP_n, $F(1, 15) = 23.06$, $MSE = 21.71$, $p < .01$, $\eta_p^2 = .61$, but not for the long FP_n, $F < 1$. In turn, the significant interaction between FP_{n-1} and cuing for the short FP_n was attributable to the fact that a 12-ms significant effect of FP_{n-1} in the neutral-cue condition, $F(1, 15) = 22.37$, $MSE = 48.85$, $p < .01$, $\eta_p^2 = .60$, was eliminated in the valid-cue condition (1 ms), $F < 1$. The corresponding ANOVA of the arcsine transformed error proportions (cf. Winer et al., 1991) yielded no significant results. However, the pattern of error data was similar to that of Experiment 1, and, consistent with the ANOVA results of Experiment 1, the interaction between FP_n and cuing approached significance, $F(1, 15) = 3.64$, $MSE = 0.010$, $p = .076$, $\eta_p^2 = .20$. There was a tendency toward more errors in the valid-cue condition than in the neutral-cue condition when FP_n was short, $F(1, 15) = 3.19$, $MSE = 0.015$, $p = .095$, $\eta_p^2 = .18$, but not when FP_n was long, $F < 1$.

CNV. As in Experiment 1, we first analyzed the development of the CNV during FP up until and including the first critical
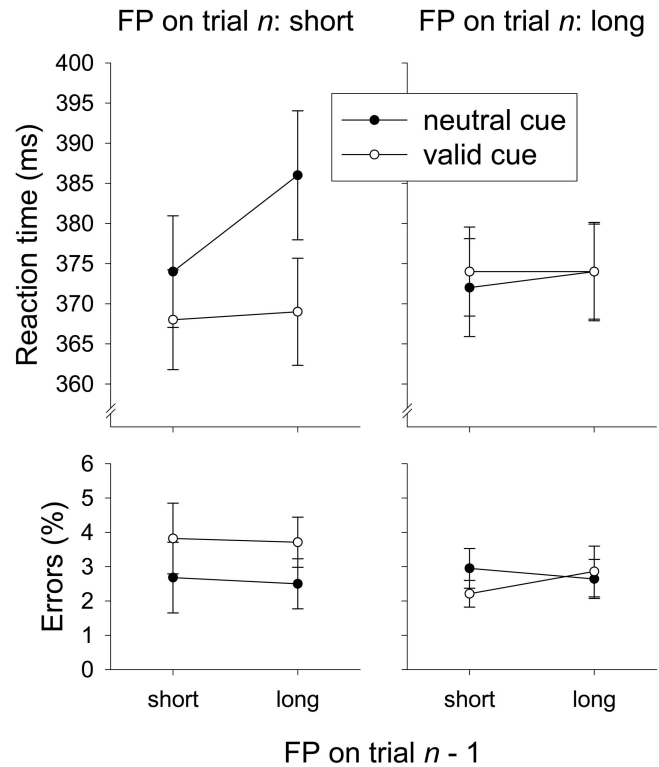

Figure 6. Mean reaction times and mean error percentages in Experiment 2 as a function of the foreperiod (FP) on trial n (from which reaction time was sampled), the FP on trial $n - 1$, and cuing. Error bars represent standard errors of the mean.

moment as a function of FP_n, FP_{n-1}, and cuing. Figure 7 shows these waveforms for the Fz and Cz electrodes. The waveforms were analyzed in four consecutive 200-ms time windows, running from 100 ms to 900 ms after the onset of S_1 (i.e., the temporal cue). Again, in the case of a short FP_n, S_2 occurred in the middle of the fourth time window.

Separate ANOVAs were conducted on the mean amplitudes obtained in each time window as a function of FP_n, FP_{n-1}, and cuing. A summary of the significant results is presented in Table 4. Three central findings of Experiment 1 were replicated. First, in approaching and bypassing the earliest critical moment, the CNV was more negative when FP_{n-1} was short than when it was long. Second, there was an interaction between cuing and FP_n that featured an early and a late effect (i.e., in Time Windows 1 and 4). Third, the effect of FP_{n-1} was approximately additive with both the effect of cuing and the effect of FP_n.

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[4] We also analyzed the CNV data relative to a 250-ms baseline preceding S_0. In this analysis, we observed a stimulus-preceding negativity (SPN) during the S_0–S_1 interval, which probably reflects an anticipation of S_1 (Brunia & Van Boxtel, 2001). It is interesting that this SPN was more negative when FP_{n-1} was short than when FP_{n-1} was long, suggesting that at least some of the conditioning effects had already been triggered by S_0. For the CNV data intervening S_1 and S_2, which we presently report, this finding implies that the effects of FP_{n-1} would have been larger if we had chosen the pre-S_0 interval as a baseline instead of the pre-S_1 interval.

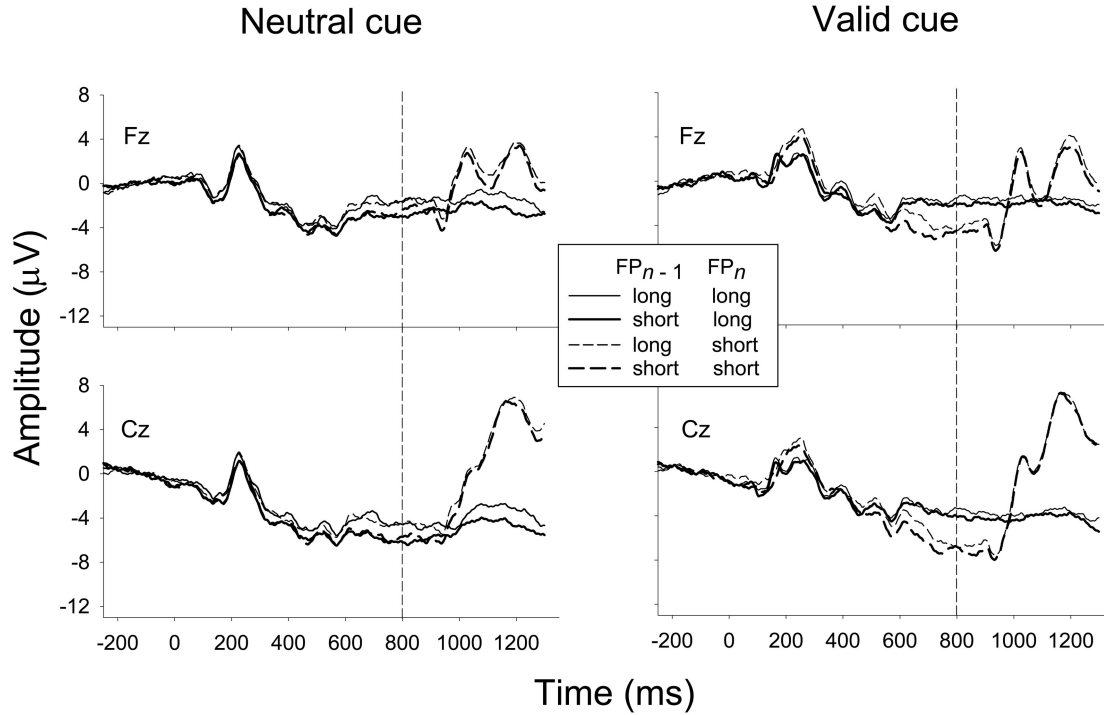## Neutral cue   Valid cue

Figure 7. Mean waveforms at frontal (Fz) and central (Cz) scalp locations in Experiment 2 up until and including the first critical moment (indicated by the broken vertical line) as a function of the foreperiod on trial n (FP$_n$) and the foreperiod on trial $n - 1$ (FP$_{n-1}$), separately for neutral and valid cues.

The interactions between cuing and FP$_n$ in the first time window for Fz and Cz reflect a greater positivity in the valid-cue condition than in the neutral-cue condition, in particular when the cue specified the early critical moment. Tests for simple main effects confirmed that at both Fz and Cz, the ERP amplitude in the first time window was more positive when the valid cue specified a short FP than when it specified a long FP, $F(1, 15) = 15.87$, $MSE = 0.62$, $p < .01$, $\eta_p^2 = .51$, for Fz, and $F(1, 15) = 9.84$, $MSE = 0.66$, $p < .01$, $\eta_p^2 = .40$, for Cz, and greater in the valid-cue condition specifying the long FP than in the neutral-cue condition, $F(1, 15) = 27.90$, $MSE = 0.38$, $p < .01$, $\eta_p^2 = .65$, for Fz, and $F(1, 15) = 26.89$, $MSE = 0.40$, $p < .01$, $\eta_p^2 = .64$, for Cz.

The interactions between cuing and FP$_n$ in the fourth time window reflect that there was a (tendency toward) a positive effect of cuing when FP$_n$ was short, $F(1, 15) = 7.74$, $MSE = 12.05$, $p < .05$, $\eta_p^2 = .34$, for Fz, and $F(1, 15) = 2.93$, $MSE = 13.59$, $p = .11$, $\eta_p^2 = .16$ for Cz, and a (tendency toward) a negative effect of cuing when FP$_n$ was long, $F(1, 15) = 2.30$, $MSE = 1.92$, $p = .15$, $\eta_p^2 = .13$, for Fz, and $F(1, 15) = 6.57$, $MSE = 6.90$, $p < .05$, $\eta_p^2 = .30$, for Cz. Thus, at both Fz and Cz, the CNV amplitude in the fourth time window was most negative when the cue specified a short FP, least negative when the cue specified a long FP$_n$, and in between when the cue was neutral. This suggests that in the neutral-cue condition, participants prepared to some extent for a possible presentation of S$_2$ at the early critical moment.

Although the effect of FP$_{n-1}$ was generally independent of cuing condition, there was one exception in the fourth time window, where the interaction between FP$_{n-1}$ and cuing was significant at Cz and approached significance at F$_z$, $F(1, 11) = 3.31$,

$MSE = 7.73$, $p = .089$, $\eta_p^2 = .23$. The effect of FP$_{n-1}$ was in both cases slightly more pronounced in the neutral-cue condition than in the valid-cue condition. However, the simple effect of FP$_{n-1}$ in the fourth time window was significant both when the cue was neutral, $F(1, 15) = 13.49$, $MSE = 2.08$, $p < .01$, $\eta_p^2 = .47$, for Cz, and $F(1, 15) = 11.28$, $MSE = 1.86$, $p < .01$, $\eta_p^2 = .43$, for Fz, and when the cue was valid, $F(1, 15) = 6.19$, $MSE = 0.70$, $p < .05$, $\eta_p^2 = .29$, for Cz, and $F(1, 11) = 4.88$, $MSE = 1.11$, $p < .05$, $\eta_p^2 = .25$, for Fz.

In a second analysis, we examined the development of the CNV during FP up until and including the second critical moment for those trials on which FP$_n$ was long, as a function of cuing and FP$_{n-1}$. Figure 8 shows these waveforms for the Fz and Cz electrodes. Separate ANOVAs were conducted on the average amplitude in each of eight 200-ms time windows, running from 100 to 1,700 ms relative to the onset of S$_1$. Table 5 shows a summary of the results. The findings were again consistent with those of Experiment 1. First, there was no interaction between cuing and FP$_{n-1}$ at either electrode or in any of the time windows. The interaction again approached significance at Cz in the third and fourth time windows, $F(1, 15) = 4.29$, $MSE = 1.95$, $p = .056$, $\eta_p^2 = .22$, and $F(1, 15) = 4.35$, $MSE = 1.55$, $p = .055$, $\eta_p^2 = .22$, respectively, but not at Fz, largest $F(1, 15) = 2.87$, $MSE = 1.17$, $p = .11$, $\eta_p^2 = .16$. Second, the effect of cuing was limited to the early time windows, indicating a greater positivity in the valid-cue condition than in the neutral-cue condition, which declined across the first two time windows at Fz and across the first four time windows at Cz. Third, the effect of FP$_{n-1}$ showed a very different time course, covering the entire S$_1$–S$_2$ interval, with a single

Table 4

Summary of Significant Effects in the Analyses of Variance of the Event-Related Potentials at Frontal (Fz) and Central (Cz) Scalp Sites in Experiment 2 Within Four 200-ms Time Windows, With Foreperiod on Trial n (FP_n), Foreperiod on Trial n − 1 (FP_{n-1}), and Cuing as Factors

	Time Window (s)			
Source	0.1–0.3	0.3–0.5	0.5–0.7	0.7–0.9
Fz				
FP_n				
η_p^2	.32			.42
MSE	0.61			6.39
F(1, 15)	7.02*			10.95**
FP_{n-1}				
η_p^2	.47	.41	.53	.42
MSE	0.63	0.74	1.32	2.19
F(1, 15)	13.10**	10.29**	16.76**	10.86**
Cuing				
η_p^2	.81	.51		
MSE	1.20	4.24		
F(1, 15)	63.75**	15.37**		
$FP_n \times FP_{n-1}$				
η_p^2				
MSE				
F(1, 15)				
$FP_n \times$ Cuing				
η_p^2	.49			.39
MSE	0.38			7.30
F(1, 15)	14.64**			9.47**
$FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
F(1, 15)				
$FP_n \times FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
F(1, 15)				
Cz				
FP_n				
η_p^2				.31
MSE				11.34
F(1, 15)				6.61*
FP_{n-1}				
η_p^2	.47	.29	.43	.50
MSE	0.70	1.03	1.71	1.84
F(1, 15)	13.39**	6.12*	11.24**	14.81**
Cuing				
η_p^2	.79	.60	.29	
MSE	1.22	7.94	7.77	
F(1, 15)	57.25**	22.16**	6.06*	
$FP_n \times FP_{n-1}$				
η_p^2				
MSE				
F(1, 15)				
$FP_n \times$ Cuing				
η_p^2	.38			.29
MSE	0.39			14.23
F(1, 15)	9.27**			5.98*
$FP_{n-1} \times$ Cuing				
η_p^2				.27
MSE				0.94
F(1, 15)				5.49*
$FP_n \times FP_{n-1} \times$ Cuing				
η_p^2				
MSE				
F(1, 15)				

* $p < .05$. ** $p < .01$.

interruption in the fifth time window at Cz, where the effect of FP_{n-1} approached significance, $F(1, 15) = 3.87$, $MSE = 1.11$, $p = .068$, $\eta_p^2 = .21$.

Finally, in the valid-cue condition with a long FP (i.e., when participants knew that the impending FP would be long), a planned comparison between the CNV amplitudes of the short and long FP_{n-1} in the fourth time window yielded a significant effect at both Fz, $F(1, 15) = 3.59$, $MSE = 0.74$, $p < .05$, $\eta_p^2 = .19$, and Cz, $F(1, 15) = 3.25$, $MSE = 0.46$, $p < .05$, $\eta_p^2 = .18$ (both tests one sided). As can be seen in both Figures 7 and 8, the CNV attained a more negative value when FP_{n-1} was short (-2.08 μV at Fz and -3.89 μV at Cz) than when FP_{n-1} was long (-1.51 μV at Fz and -3.46 μV at Cz).

LRP. Figure 9 shows the LRP amplitude as a function of cuing, FP_n, and FP_{n-1}. The ANOVA of these data up until and including the first critical moment, with cuing, FP_n, and FP_{n-1} as factors, revealed an overall negative deflection of the LRP that increased in strength across subsequent time windows. The F values increased from 23.48 for the first time window to 54.55 for the fourth time window (all p values < .01; smallest $\eta_p^2 = .61$). Furthermore, there was a significant effect of FP_n in the fourth time window, $F(1, 15) = 7.54$, $MSE = 0.36$, $p < .05$, $\eta_p^2 = .33$, reflecting a more negative LRP in the case of a short FP_n than in the case of a long FP_n. This effect was modified by FP_{n-1}, $F(1, 15) = 4.66$, $MSE = 0.12$, $p < .05$, $\eta_p^2 = .24$, indicating that in the case of a short FP_{n-1}, the LRP was more negative for a short FP_n (-1.01 μV) than for a long FP_n (-0.59 μV), whereas this difference was less pronounced after a long FP_{n-1} (-0.86 μV vs. -0.70 μV, respectively). Furthermore, there was also a tendency toward a significant interaction between cuing and FP_n in the fourth time window, $F(1, 15) = 4.28$, $MSE = 0.55$, $p = .056$, $\eta_p^2 = .22$, indicating that the LRP amplitude was more negative for a short FP_n (-1.09 μV) than for a long FP_n (-0.53 μV) when the cue was valid but not when the cue was neutral (-0.78 μV vs. -0.76 μV, respectively). Note that this interaction is similar to the corresponding interaction on the CNV in that the LRP in the fourth time window was most negative when the valid cue specified the short FP, least negative when it specified the long FP, and in between when the cue was neutral.

The ANOVA of the LRP amplitude up until and including the second critical moment for the long FP_n condition, with cuing and FP_{n-1} as factors (Figure 9, bottom panel), revealed a negative deflection of the LRP in all time windows, smallest $F(1, 15) = 21.34$, $MSE = 1.37$, $p < .001$, $\eta_p^2 = .59$. Furthermore, there was a trend toward a significant main effect of cuing in the fourth time window, $F(1, 15) = 3.51$, $MSE = 0.47$, $p = .081$, $\eta_p^2 = .19$, but no other effects approached significance, largest $F(1, 15) = 1.91$, $MSE = 0.52$, $p = .19$.

Electrophysiological–behavioral correspondence. As in Experiment 1, we calculated across participants and separately for each of the eight experimental conditions mean RT and the corresponding mean CNV amplitude, averaged across a 200-ms time window surrounding the imperative moment. The Pearson product–moment correlation between these variables was .86 at Fz, $F(1, 6) = 17.35$, $MSE = 9.18$, $p < .01$, adjusted $R^2 = .70$, and .73 at Cz, $F(1, 6) = 6.76$, $MSE = 16.80$, $p < .05$, adjusted $R^2 = .45$. After we applied a log transform to the CNV amplitudes (see Figure 10), the correlations increased to .91 at Fz (adjusted $R^2 = .80$) and to .78 at Cz (adjusted $R^2 = .55$). This increase was
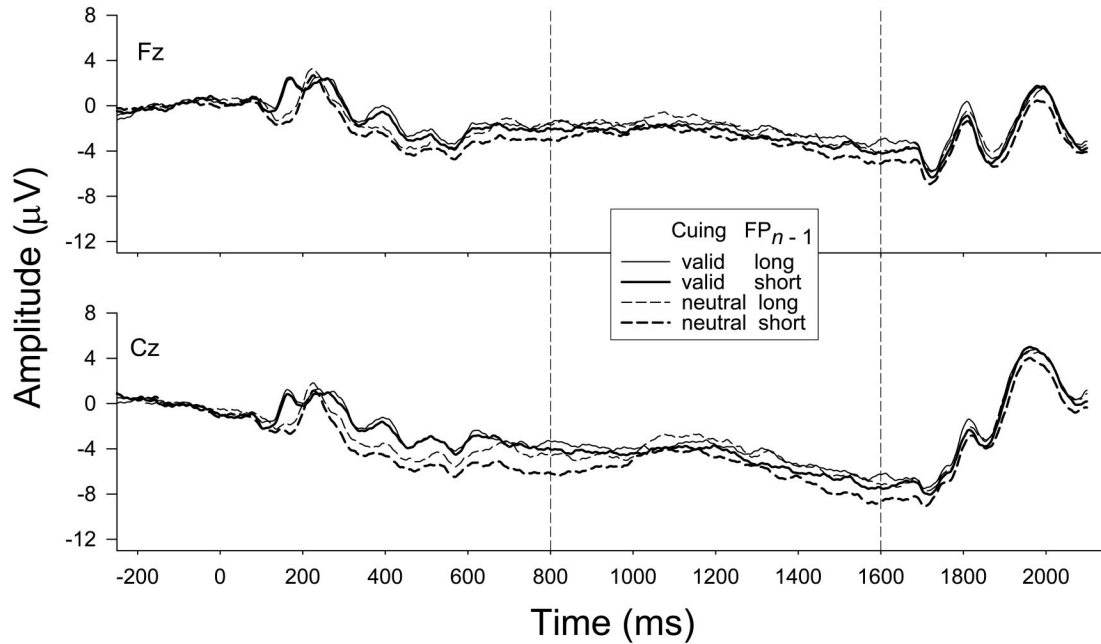
Figure 8. Mean waveforms at frontal (Fz) and central (Cz) scalp locations in Experiment 2 up until and including the second critical moment as a function of the foreperiod on trial $n - 1$ (FP$_{n-1}$) and cuing. Vertical broken lines correspond to the critical moments; only the conditions with a long foreperiod on trial n are shown.

significant by Williams's statistic (Steiger, 1980) at Cz, $T_2(5) = 2.52$, $p < .05$, and approached significance at Fz, $T_2(5) = 1.61$, $p = .084$ (both tests one sided).

Discussion

Overall, the findings of Experiment 2 were very similar to those of Experiment 1, although the effect sizes were generally somewhat smaller. Thus, the additional requirement in Experiment 2 to switch the responding hand on a trial-by-trial basis did not compromise the nonspecific preparatory processes of present interest but may have reduced their expression in the dependent variables. Although the behavioral findings of Experiment 2 were very similar to those of Experiment 1, some minor differences may be noted. First, cuing completely reduced the sequential effect on RT for the short FP$_n$ in Experiment 2, whereas some residual effect remained in Experiment 1. Second, consistent with earlier studies (e.g., Los et al., 2001; Van der Lubbe et al., 2004; Zahn, 1963), Experiment 2 showed no sequential effect on RT for the longest FP$_n$, whereas a small sequential effect was observed in Experiment 1. Third, in Experiment 2, the effect of cuing on the error rate for the short FP$_n$ was not more than a trend, whereas it was significant in Experiment 1. However, these differences were all minor and do not suggest any fundamental difference in the underlying processing dynamics, so we do not discuss them any further. Instead, we turn to the main question of whether the effects of cuing and FP$_{n-1}$ stem from the same process (single-path hypothesis) or from different processes (dual-path hypothesis).

Strong support for the dual-path hypothesis was again provided by the CNV amplitude data. During the entire S_1–S_2 interval, there was a clear effect of FP$_{n-1}$, which was hardly modified by cuing. In fact, the only significant violation of additivity was observed at Cz in the fourth time window, where the effect of FP$_{n-1}$ was larger

in the neutral-cue condition than in the valid-cue condition. However, the specific effect of FP$_{n-1}$ was significant even in the latter condition, indicating that preknowledge of the duration of the impending FP did not erase the effect of FP$_{n-1}$. These findings argue against the assumption of the single-path hypothesis that the participant's uncertainty in the neutral-cue condition about the impending imperative moment induces a bias to initially orient to the critical moment that was the imperative moment on the last trial. If that were the case, the effect of FP$_{n-1}$ should have been eliminated in the valid-cue condition, in which there was no uncertainty about the impending imperative moment, contrary to what we found. Furthermore, we again observed that the effect of cuing on the CNV amplitude was limited to the fourth time window provided that FP$_n$ was short. This phasic influence of cuing contrasts with the tonic influence of FP$_{n-1}$, once again suggesting that these factors affect different processes, here interpreted as temporal orienting and trace conditioning, respectively.

In further agreement with Experiment 1, we observed that the CNV amplitude at the imperative moment proved a good predictor of RT, especially after a logarithmic transformation. In comparison with Experiment 1, the observed correlations were somewhat lower, though, and relied more strongly on the relatively long RT and low CNV amplitude observed in the neutral-cue condition with a short FP$_n$ and a long FP$_{n-1}$. This reduced correlation may be due to the more complicated procedure that was followed in Experiment 2, but the general pattern of results closely replicates the pattern found in Experiment 1.

With respect to the LRP data, we observed a clear negative deflection throughout the entire S_1–S_2 interval, which was opposite to the positive deflection observed in Experiment 1. Thus, by requiring participants to switch between responding hands on a trial-by-trial basis rather than to switch between responding hands

Table 5

Summary of Significant Effects in the Analyses of Variance of the Event-Related Potentials at Frontal (Fz) and Central (Cz) Scalp Sites in Experiment 2 Within Eight 200-ms Time Windows, With Foreperiod on Trial n − 1 (FP_{n-1}) and Cuing as Factors

Source	Time window (s)							
	0.1–0.3	0.3–0.5	0.5–0.7	0.7–0.9	0.9–1.1	1.1–1.3	1.3–1.5	1.5–1.7
Fz								
FP_{n-1}								
η_p^2	.26	.34	.38	.44	.38	.39	.50	.56
MSE	0.53	0.54	0.71	1.10	0.80	1.17	0.98	0.76
$F(1, 15)$	5.22*	7.68*	9.19**	11.75**	9.21**	9.47**	14.93**	19.10**
Cuing								
η_p^2	.59	.44						
MSE	0.95	2.50						
$F(1, 15)$	21.56**	11.70**						
FP_{n-1} × Cuing								
η_p^2								
MSE								
$F(1, 15)$								
Cz								
FP_{n-1}								
η_p^2	.38	.39	.35	.46	.21	.37	.59	.59
MSE	0.43	0.37	0.62	0.98	1.11	1.20	0.91	0.78
$F(1, 15)$	9.32**	9.59**	8.03*	12.85**	3.87	8.66*	21.79**	21.93**
Cuing								
η_p^2	.59	.45	.37	.31				
MSE	0.98	6.43	6.59	6.90				
$F(1, 15)$	21.27**	12.31*	8.63*	6.57*				
FP_{n-1} × Cuing								
η_p^2								
MSE								
$F(1, 15)$								

* $p < .05$.   ** $p < .01$.

after each series of six blocks, we achieved our aim of eliciting the common negative-going LRP, reflecting ongoing motor preparation (for reviews, see Coles, 1989; Eimer, 1998). However, even under these favorable conditions, we again failed to observe that the main effect of FP_{n-1} on the CNV had a counterpart on the LRP. Instead, we observed a significant interaction effect between FP_{n-1} and FP_n in the fourth time window of the LRP that had no counterpart on the CNV, indicating an effect of FP_{n-1} when FP_n was short but not when FP_n was long. Note that this interaction effect must be related to the onset of S_2 itself, because the levels of FP_{n-1} were not differentially predictive for the duration of the impending FP_n. Whatever the basis of this effect, it should be clear that it is not related to the preparatory processing of present interest. Furthermore, the interaction effect between cuing and FP_n approached significance in the fourth time window and exhibited the same pattern as its counterpart on the CNV. In particular, both measures revealed that the negative deflection in the fourth time window was largest when the cue specified the short FP, smallest when it specified a long FP, and intermediate when it was neutral. This similarity suggests that temporal orienting is at least partially motoric in nature.

In conclusion, the CNV data of Experiment 2 were highly consistent with those of Experiment 1 and further supported the dual-path hypothesis. Also, whereas it is clear that none of the preparatory effects on the CNV involving FP_{n-1} had a counterpart on the LRP, the interaction between cuing and FP_n seemed to be reflected on both measures. Thus, the LRP findings revealed another dissociation between the effects of cuing and FP_{n-1}, which adds to the evidence for the dual-path hypothesis.

General Discussion

In this study, we aimed at identifying intentional and unintentional influences to the state of nonspecific preparation. For this purpose, we examined how sequential effects of FP and effects of temporal cuing combine to affect preparation-related brain potentials in addition to behavioral measures. Consistent with previous studies, we observed asymmetrical sequential effects on RT when the cue was neutral (e.g., Los et al., 2001; Woodrow, 1914; Zahn et al., 1963); these effects were strongly reduced in Experiment 1 and eliminated in Experiment 2 when the cue was valid (Los & Van den Heuvel, 2001). The major finding of this study was that cuing and FP_{n-1} left a different signature on the CNV, which we used as a general index of nonspecific preparation. This finding strongly suggests that the effects of cuing and FP_{n-1} are expressions of different mental operations that are referred to as temporal orienting, an intentional contribution to nonspecific preparation, and trace conditioning, an unintentional contribution, respectively.
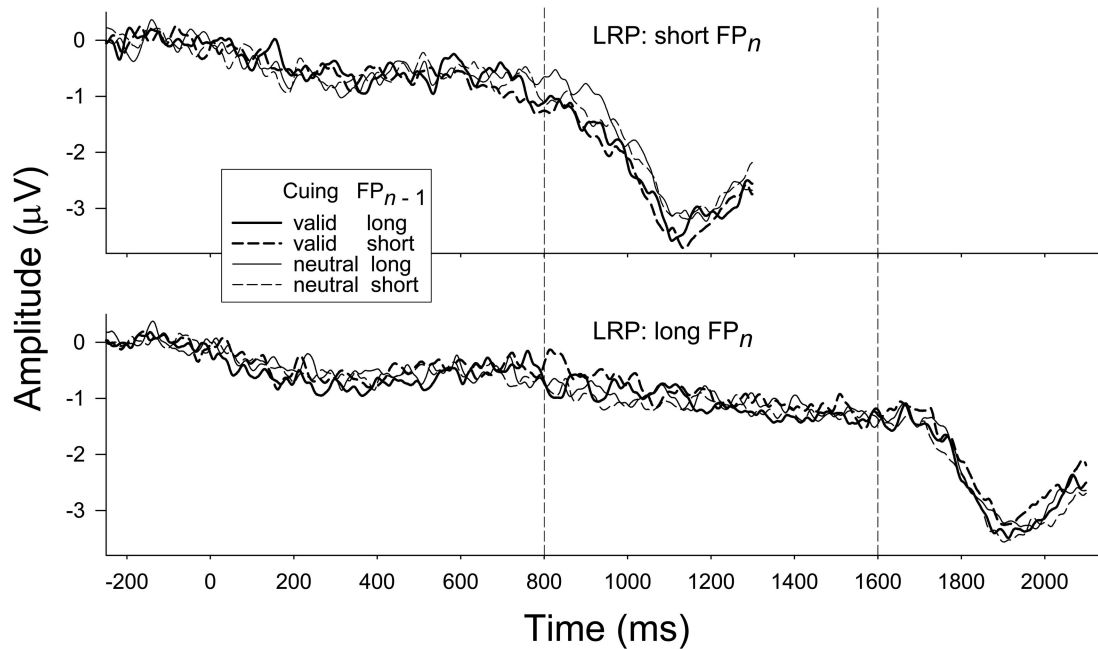
Figure 9. Mean lateralized readiness potential (LRP) waveforms in Experiment 2 as a function of the foreperiod on trial *n* (FP$_n$), the foreperiod on trial *n* − 1 (FP$_{n-1}$), and cuing. Vertical broken lines correspond to the critical moments.

Intentional and Unintentional Influences to Nonspecific Preparation

Effective temporal orienting, based on a valid cue, requires that participants are capable of translating the symbolic content of the cue into a heightened state of preparation for the specified moment in time. Strong support for this two-step "interpret–orient" processing cycle was provided by two components in our CNV data, which emerge when comparing the valid-cue condition with the neutral-cue condition. The first component relates to the interpretation of the information provided by the valid cue. Both experi-
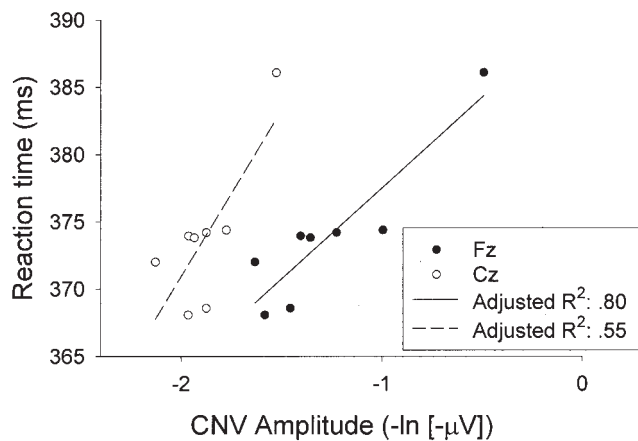

Figure 10. The relation between mean reaction time for the eight experimental conditions and the logarithmically transformed contingent negative variation (CNV) amplitude averaged across the 200-ms interval around the corresponding imperative moment in Experiment 2. Fz = frontal scalp location; Cz = central scalp location.

ments showed a greater positivity of early components of the ERP, starting at the frontocentral N1, when the cue was valid versus when it was neutral. This early effect is likely to reflect the discriminative processing of the symbolic content of the valid cue over and above the nondiscriminative processing of the neutral cue. The information gained by this additional processing leads up to temporal orienting, the second component of the two-step processing cycle. Temporal orienting is reflected by the amplitude of the CNV at the early critical moment, which was larger when this moment was specified by the cue than when it was not specified by the cue. Apparently, participants used the information provided by the valid cue to enhance their state of nonspecific preparation at the early critical moment. It is important to note that these two intentional components were always separated by at least a 200-ms time window during which there was no effect of cuing. Thus, the second component of intentional processing cannot be interpreted as a mere continuation of the first component, lending credibility to the two-step interpret–orient processing cycle, of which the second component is adaptively timed to the appearance of S$_2$.

Crucially, this study revealed that the effect of FP$_{n-1}$ on the CNV was largely independent of that of cuing. Both experiments showed that the effect of FP$_{n-1}$ was not eliminated in any condition by the information provided by a valid cue. This observation was particularly telling for the long FP$_n$ condition, where we observed an effect of FP$_{n-1}$ at the early critical moment even when participants were informed that the impending FP would be long. Also, in the short FP$_n$ condition, the strong contribution of the valid cue to the amplitude of the CNV at the early critical moment (i.e., the imperative moment) did not abolish the contribution of the sequential effect of FP to this amplitude. Finally, the contributions of FP$_{n-1}$ and cuing to the CNV amplitude exhibited qualitatively different time courses. The effect of FP$_{n-1}$ was tonic

in that it pervaded the FP, regardless of its duration, after its incipience sometime after the onset of S_1. By contrast, the effect of cuing on the CNV was phasic in that it was observed only in the temporal proximity of the early critical moment, when the impending FP_n was short.

These findings strongly suggest that the origin of the effect of FP_{n-1} is different from that of cuing. Indeed, if the effect of FP_{n-1} reflected a strategic use of temporal orienting in the neutral-cue condition, driven by uncertainty about the timing of S_2, it should have been eliminated after a valid cue, contrary to what we found. Therefore, given that the effect of cuing reflects an intentional influence of temporal orienting, our findings suggest that the effect of FP_{n-1} is unintentional in nature. This supports the assumption of the trace-conditioning account that the sequential effect of FP reflects an unintentional consequence of the inhibitory process that adjusts the state of conditioning during FP (Los & Van den Heuvel, 2001).

This distinction between intentional and unintentional processes of nonspecific preparation complements the behavioral evidence for this view presented by Los and Van den Heuvel (2001), which we discussed in the introduction. More recently, Lewis and Miall (2003) provided confirmatory evidence for distinct timing mechanisms in a review of over 30 functional magnetic resonance imaging studies (but see Macar et al., 2002, for a deviating view). From the differential involvement of brain regions in different timing tasks, they inferred a distinction between what they called an automatic timing mechanism and a cognitively controlled timing mechanism. In particular, the automatic timing mechanism is called on to the extent a task requires the timing of relatively brief intervals, indicated by a motor response, and embedded in a predicable (or continuous) sequence. The cognitive timing mechanism is called on to the extent a task requires the timing of long intervals, not indicated by motor responses, and embedded in unpredictable sequences. Even though the brain regions commonly activated under the different task conditions showed some overlap (in particular, in the bilateral supplementary motor area and lateral premotor areas), there was a clear trend toward an implication of motor-related areas in automatic-timing tasks, whereas regions more remote to the motor system, involving prefrontal and parietal regions, were implicated in cognitive timing tasks.

According to the taxonomy of Lewis and Miall (2003), the task of the present study seems to be a prototypical automatic-timing task in the neutral-cue condition, while the valid cue may introduce a cognitively controlled timing mechanism as an additional process. What we propose, then, is that the trace conditioning and temporal orienting processes as we introduced them correspond to Lewis and Miall's automatic and cognitively controlled timing mechanisms, respectively. In addition, our data suggest that these processes do not necessarily operate in a mutually exclusive fashion but may contribute to behavior in parallel.

The Locus of Temporal Orienting and Trace Conditioning

The CNV amplitude data of this study yielded valuable insights into the distinct contributions to nonspecific preparation but did not allow a functional localization of these contributions. For this reason, we examined to what extent the CNV effects are also reflected on the LRP, which is widely considered to be a pure measure of central motor activation (e.g., Coles, 1989; Eimer, 1998). The hallmark of the LRP is a negative deflection during the preparation and execution of a hand response, reflecting more activation of the contralateral motor cortex as compared with the ipsilateral motor cortex. This negative deflection was clearly present during the entire FP in Experiment 2, indicating ongoing motor preparation of the responding hand. Therefore, we used the LRP data of Experiment 2 to examine possible modifying influences of cuing and FP_{n-1}.

The results of Experiment 2 showed that whereas cuing had corresponding effects on the CNV and the LRP, this was not the case for FP_{n-1}. This dissociation may be taken as further evidence for a distinction between intentional and unintentional influences to nonspecific preparation, in that a valid cue enhances motor preparation but a short FP_{n-1} does not. However, this conclusion should be regarded as tentative at present because the relevant interaction effect between cuing and FP_n in the fourth time window of the LRP fell just short of statistical significance. Furthermore, whereas it is clear that the presence of a factor influence on the LRP amplitude reflects motor preparation (e.g., Leuthold et al., 1996; Sangals et al., 2002), the reverse is much less clear. For instance, in a well-controlled study, Sommer, Leuthold, and Ulrich (1994) failed to find any evidence for an influence of instructed response force on the LRP amplitude during FP, which suggests that the specification of force parameters are not expressed in the LRP amplitude during FP. It is conceivable that something similar applies to FP_{n-1}, given the evidence that response force, as a dependent variable, is affected by FP (e.g., Jaśkowski & Verleger, 1993; Mattes & Ulrich, 1997; Van der Lubbe et al., 2004) and, as an independent variable, modifies the effect of FP on RT (Sanders, 1980). In view of these findings, it cannot be excluded that the preparatory effect of FP_{n-1} is motoric after all, although it is not reflected in the LRP amplitude.

The LRP findings of Experiment 1 do not help clarify this picture, although they are interesting in themselves. In this experiment, we observed a positive deflection of the LRP throughout the short FP and during the first 1,200 ms of the long FP. This positivity seems puzzling at first but may be explained by considering possible consequences of our procedure of fixing the responding hand within a block of trials. This procedure may have resulted in a tonic hemispheric difference during a block of trials, yielding a baseline relative to which a negative deflection of the FP LRP may have failed to materialize. Against this background of a tonic hemispheric difference, a positive-going LRP then may reflect that the responding hand is subject to inhibition after the presentation of S_1 to prevent premature responding during the FP.

Although this is a post hoc account, it makes sense both theoretically and empirically. It makes sense theoretically in that it relates to the assumption of the trace conditioning account that in bypassing a critical moment, the state of conditioning corresponding to that moment is subject to inhibition. The LRP might reflect this inhibition, given recent insights that apart from activating influences stemming from one hemisphere, the LRP also reflects inhibitory influences from the opposite hemisphere (e.g., Tandonnet et al., 2003; Taniguchi, Burle, Vidal, & Bonnet, 2001). The proposed account makes sense empirically in that it is consistent with several findings from psychophysiology showing a prominent role of inhibition during FP. For instance, during this interval, physiological correlates of preparation, including heart rate (e.g., Bohlin & Kjellberg, 1979; Jennings & Van der Molen, 2002; Jennings, Van der Molen, & Steinhauer, 1998) and pupil diameter (e.g., Jennings et al., 1998), show influences of inhibition relative

to their appropriate baselines. Similar results have been obtained in studies that probed the state of preparation during FP experimentally by stimulating the Achilles' tendon reflex (e.g., Brunia & Boelhouwer, 1988; Requin et al., 1991) or the primary motor cortex through transcranial magnetic stimulation (e.g., Burle, Bonnet, Vidal, Possamaï, & Hasbroucq, 2002; Hasbroucq, Kaneko, Akamatsu, & Possamaï, 1997; Hasbroucq et al., 1999). These findings have been interpreted as reflecting inhibition of the corticospinal pathway (e.g., Hasbroucq et al., 1997, 1999; Tandonnet et al., 2003), which may serve to keep the motor system in check during FP (Brunia, 1993, 1999; Brunia & Van Boxtel, 2000).

Together, the LRP findings of this study had some intriguing features, which may be relevant for future explorations of inhibitory contributions to nonspecific preparation. However, they did not converge onto a clear answer with respect to the functional locus of the effects of cuing and FP_{n-1}.

Integrating Intentional and Unintentional Influences

The CNV amplitude data of the present study supported the dual-path hypothesis but not our hypothesis that the influences of trace conditioning and temporal orienting combine underadditively to determine the state of nonspecific preparation (cf. Los & Van den Heuvel, 2001). What remains to be explained, then, is the relation between nonspecific preparation and behavior. The problem is that during FP, cuing and FP_{n-1} had roughly additive influences on the CNV amplitude, but after FP, they strongly interacted on RT.

To solve this problem, we propose a dual-path solution that relies on two assumptions. First, the influences of temporal orienting and trace conditioning to nonspecific preparation have an independent neural origin. According to the physics of electrical volume conduction (e.g., Scherg, 1990; Sternberg, 2001), the influences of independent neural sources should combine additively in the ERP. Consistent with this principle, we observed approximately additive effects of cuing and FP_{n-1} on the CNV. Second, the behavioral expression of the state of nonspecific preparation on RT is subject to diminishing returns. This implies that one additional unit of preparation leads to a reduction in RT that is greater if the initial state of preparation is low than if it is high. Consistent with this implication, we observed that the correlation between the CNV amplitude at the imperative moment and the corresponding RT was higher when the CNV values were presented on a logarithmic scale than when they were presented on a linear scale.

We realize that this solution is idealized because the additivity of effects of cuing and FP_{n-1} was not perfect. However, the solution has its merits in emphasizing the distinction between unintentional and intentional contributions to nonspecific preparation, which is the major finding of this study. Furthermore, the law of diminishing returns has a wide general validity (e.g., Landauer, 1975), and its present application seems particularly plausible in view of the increasing resistance of RT when pushed toward its absolute floor.

Conclusions

This study showed that the effects of cuing and FP_{n-1} on the CNV had highly distinct time courses and were additive in almost all time windows. These findings strongly suggest that the contri-

bution of FP_{n-1} to the state of nonspecific preparation is distinct from that of cuing. In particular, given that the effect of cuing reflects temporal orienting, an intentional contribution to nonspecific preparation, the effect of FP_{n-1} is likely to be unintentional in nature and caused by a process of trace conditioning. Our main findings therefore support a dual-path architecture in which temporal orienting and trace conditioning contribute independently to the state of nonspecific preparation. The additional finding of a strong interaction between cuing and FP_{n-1} on RT (given a short FP_n) is not inconsistent with this view, as it can be explained by assuming that the behavioral expression of nonspecific preparation is subject to diminishing returns.

More generally, the present study showed the merits of the concept of trace conditioning for understanding sequential learning in nonspecific preparation. In the behavioral literature, sequential effects of FP have been studied since the seminal work of Woodrow (1914; e.g., Baumeister & Joubert, 1969; Drazin, 1961; Karlin, 1959; Zahn et al., 1963), yet an account of this phenomenon in terms of trace conditioning has not been considered until recently (Los, 1996; Los & Van den Heuvel, 2001; Los et al., 2001). By contrast, in the electrophysiological literature, the CNV has been characterized as a "conditioned brain response" (p. 382) by Walter et al. (1964) in their original report (see also Low, Borda, Frost, & Kellaway, 1966). Yet the subsequent development of this view did not incorporate sequential effects of FP because it occurred within the context of more typical conditioning paradigms with a biologically relevant S_2 (e.g., Backs & Grings, 1985; Flor et al., 1996; Hablitz, 1973; Lumsden, Howard, & Fenton, 1986; Regan & Howard, 1995). The present results suggest that Walter et al.'s original interpretation was a powerful one and that processes of trace conditioning play a general role during the preparation interval.

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