
EARLY CAREER AWARD

The functional significance of ERP effects during mental rotation

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Abstract

In a parity judgment task, the ERPs at parietal electrode sites become more negative as more mental rotation has to be executed. This article provides a review of the empirical evidence regarding this amplitude modulation. More specifically, experiments are reported that validate both the functional relationship between mental rotation and the amplitude modulation as well as the temporal relationship both in single- and in dual-task situations. Additionally, ERP effects are reported in the psychological refractory period (PRP) paradigm with mental rotation as the second task. Finally, unresolved issues are discussed that, I hope, might stimulate future research.

Descriptors: Event-related brain potentials (ERP), Cognition, Mental rotation, Processing related negativity, Mental chronometry, Psychological refractory period (PRP)

One of the basic goals of cognitive electrophysiology is to establish the functional significance of a certain event-related potential (ERP) effect, that is, describing the ERP effect in terms of specific cognitive operations or processes that elicit it (for a very profound discussion, see Rugg & Coles, 1995). If the functional significance is established, the ERP effect then can be used as a “tool” to investigate the cognitive operation in more detail. Because the cognitive operation cannot be observed directly, the ERP effect then can be used to indicate, for example, the presence or absence of the cognitive operation in specific situations, even without the need of an overt response. Moreover, the latency of the ERP effect can tell us something about the latency of the cognitive operation.

To give a recent example of this approach, the functional significance of the N400 amplitude modulation was established as reflecting the semantic relatedness between a word and its context (see, e.g., Kutas & van Petten, 1994; Osterhout & Holcomb, 1995). Assume a condition in which a word cannot be identified due to an attentional overload manipulation. The conclusion that if the semantic association between this unidentified word and a word presented later affects the N400 evoked by the subsequent word, then the unidentified word was processed semantically (and can

prime the subsequent word; see, e.g., Rolke, Heil, Streb, & Hennighausen, 2001) can be drawn *only if* the functional significance mentioned above was established previously.

Thus, to establish the functional significance of a certain ERP effect is not only worth the effort from a purely psychophysiological point of view. Moreover, it is the requisite to enlarge the focus of research from a psychophysiological one (i.e., “What is measured by the ERP effect?”) to a cognitive one (i.e., “What do we learn about the cognitive operation by measuring the ERP effect?”).

In the following, a series of experiments is presented aimed to establish the functional significance of the ERP effects at parietal electrode leads during mental rotation of characters.¹ The experiments validated the functional as well as the temporal relationship between the cognitive process of mental rotation and the orientation-related amplitude modulation that is observable in this task. Additionally, recent experiments directly focusing on the cognitive aspects of mental rotation are reported. Finally, a number of unresolved issues are discussed that, I hope, might stimulate future research.

ERP Effects during Mental Rotation

If characters are presented in a number of different orientations in either their regular format or left–right mirror reversed, the time to decide upon the parity of the character increases monotonically with the angular displacement from the upright (Cooper & Shep-

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¹This review is restricted to ERP effects during mental rotation tasks with *characters* as stimuli. Moreover, the results reported are limited to ERPs obtained at the mid-parietal electrode lead Pz. Both aspects are discussed at the end of this article.

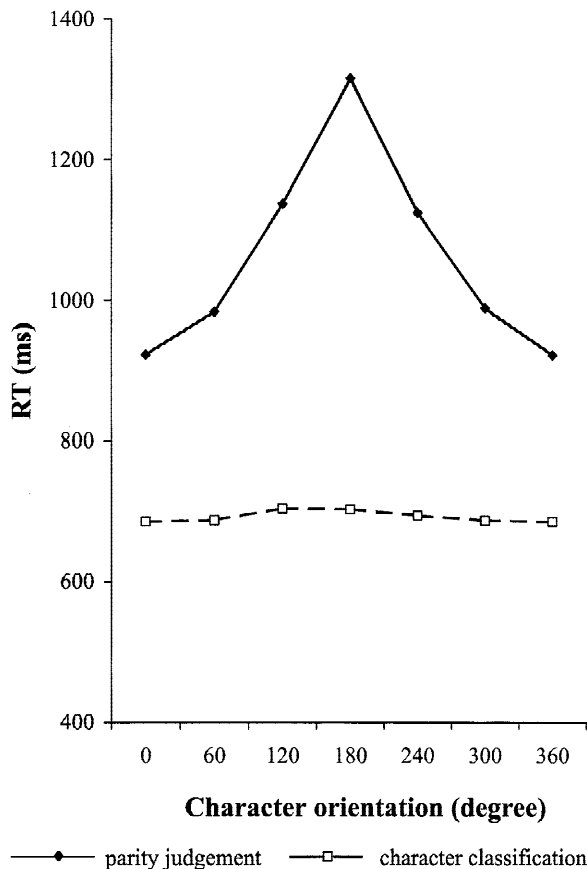


Figure 1. Mean response times as a function of character orientation and type of task (parity judgement vs. character classification).

ard, 1973). If, however, subjects have to classify the character as either a letter or a digit, response time is, at least after some practice trials, independent of the character's orientation (see Figure 1).

The most salient interpretation of this effect is that subjects can classify, but are not able to judge the parity of a character without an "orientation-normalization" process. It is generally assumed (see, e.g., Shepard & Cooper, 1982) that a representation of the letter is mentally rotated in a continuous way to align it with its upright orientation in which it is represented in memory (see, e.g., Cooper, 1976; Heil, Bajric, Rösler, & Hennighausen, 1997). This process, referred to as mental rotation, takes an amount of time that is proportional to the angular disparity from the upright.

Although the term *mental rotation* is used throughout this article, none of the underlying logic of the experiments reported here requires the full mental rotation hypothesis, that is, the assumption of a continuous spatial transformation. These experiments can be reframed as an empirical investigation of the functional significance of the ERP effects during the orientation-normalization process rather than as an investigation of the functional significance of the ERP effects during mental rotation.

The electrophysiological correlates of the mental rotation process with characters as stimuli were first explored² by Wijers,

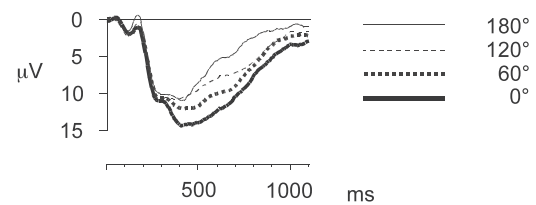


Figure 2. Grand average event-related potentials obtained from electrode position Pz as a function of character orientation. Negativity is plotted up. Character presentation at $t = 0$ s. Data from the experiment of Heil et al. (1996).

Otten, Feenstra, Mulder, and Mulder (1989) with their results replicated by Perronet and Farah (1989) and by Rösler, Schumacher, and Sojka (1990). The standard ERP effect most reliably obtained at parietal electrode leads (see Figure 2) consists of a pronounced positive component (a P300) evoked by the presentation of the character. The amplitude of this positivity is inversely related to the character orientation, that is, the amplitude becomes relatively *more negative* with increasing angular disparity from the upright.

Wijers et al. (1989) argued that the gradual decrease of the positivity is caused by a modulation of a slow negativity that is superimposed on the simultaneously prevailing P300, which itself is independent of character orientation. Wijers et al. (1989) and Rösler et al. (1990) suggested that the negativity should be understood as a direct electrophysiological correlate of the mental rotation process itself. Because the constant positivity and the orientation-dependent negativity are assumed to overlap in time, the decrease in positivity with increasing angular orientation is measured as the net effect.

If valid, this, of course, would mean that the amplitude modulation could be used as a neurophysiological indicator of the cognitive process of mental rotation. For example, the ERP effect thus could provide independent evidence of whether or not mental rotation is present in a certain task where it was suggested to be. Moreover, the *onset* of the effect could be used as a chronopsychophysiological marker for the onset of the process. Therefore, quite important debates in experimental psychology could benefit from that finding.

Unfortunately, however, Wijers et al. (1989), Perronet and Farah (1989), and Rösler et al. (1990) provided no empirical evidence whatsoever for the assumptions mentioned above. The main goal of this article is to review the empirical evidence obtained during the last couple of years. Therefore, first the evidence regarding the functional relationship between mental rotation and the amplitude modulation is presented. Thereafter, recent experimental data regarding the temporal relationship are presented, and, finally, a first attempt is reported to use the amplitude modulation as a psychophysiological marker of mental rotation in order to address a theoretically important but empirically unresolved problem in experimental psychology.

The Functional Relationship between Mental Rotation and the Amplitude Modulation

The functional relationship can be understood as the question of whether or not the amplitude modulation can indeed be traced back to the process of mental rotation, or whether other processes

²Stuss, Sarazin, Leech, and Picton (1983) compared the ERP effects of mental rotation and picture naming but did not manipulate the orientation of the stimuli systematically.

involved in the task might be responsible for the effect to occur. If the functional relationship is given, and that is the simplest line of reasoning, then the amplitude modulation should be absent, if the task can be solved without mental rotation. As mentioned above, response times to classify a disoriented (and probably even mirror-reversed) character as a letter or a digit are independent of the character's orientation (see, e.g., Corballis & Nagourney, 1978; Heil, Bajric, Rösler, & Hennighausen, 1996). As a consequence, it is assumed that no mental rotation is involved in character classification. Therefore, no amplitude modulation as a function of character orientation should be present.

We realized mental rotation as a two-alternative forced choice (2AFC) go–nogo task (Heil, Rauch, & Hennighausen, 1998). The stimuli were the alphanumeric characters F, P, R, G, Q, 2, 3, 4, 5, and 7. Each character was presented either in its normal version or in mirror image, rotated 30°, 90°, or 150° either clockwise or counterclockwise from the upright position. Character classification (letter versus digit) determined go versus nogo, whereas character's parity (normal versus mirror-reversed) determined the responding hand (left versus right). So, for example, for one subject, the instruction could read: "Press a left-hand button in the case of a normal digit but a right-hand button in the case of a mirror-reversed digit. Do not respond at all, however, if a—normal or mirror-reversed—letter is presented."

Obviously, go trials involve character classification but also mental rotation in order to determine the responding hand. Nogo trials, however, can be solved solely on the basis of character classification with no mental rotation involved. Therefore, in concordance with the theoretical assumptions of Wijers et al. (1989) and Rösler et al. (1990), the amplitude modulation as a function of character orientation should be present for go trials but should be absent for nogo trials. The results fully confirmed these predictions (see Figure 3).

The simplest consequence of the functional relationship assumption was therefore validated (see also Heil et al., 1996), that is, the amplitude modulation was absent when the task was solved without mental rotation. However, in the task used by Heil, Rauch, & Hennighausen (1998), go trials and nogo trials do not only differ as to whether the process of mental rotation was present or absent, but also as to whether a response had to be executed or withheld. The question of response execution itself, however, should be completely irrelevant for the presence or absence of the amplitude modulation. That is, if mental rotation was to be used in a nogo

condition, the amplitude modulation should be present despite the absence of response execution.

Therefore, we realized mental rotation in a different version of a 2AFC go–nogo task (Heil, Rauch, & Hennighausen, 1998) in which mental rotation should be present for both go and nogo trials. The same stimuli were presented as in the task described before. The parity of the character now, however, determined go versus nogo, whereas character classification determined the responding hand. So, for example, for one subject, the instruction could read: "Press a left-hand button in the case of a normal digit but a right-hand button in the case of a normal letter. Do not respond at all, however, if a mirror-reversed character—letter or digit—is presented."

In this version of the task, obviously, both go and nogo trials involve character classification and also mental rotation in order to determine the response. In concordance with the theoretical assumptions, the amplitude modulation as a function of character orientation should now be present for both go and nogo trials. The results, in fact, fully confirmed these predictions (see Figure 4). The question of whether a manual response had to be executed or had to be withheld turned out to be completely irrelevant for the presence of the amplitude modulation.

To summarize these findings, the study of Heil, Rauch, and Hennighausen (1998) provided evidence that the amplitude modulation as a function of character orientation is absent if the task could be solved without mental rotation. If mental rotation, however, is needed to solve the task, then the amplitude modulation is present irrespective of whether a response is executed or withheld. These data provide first evidence suggesting that mental rotation might constitute both a necessary as well as a sufficient requisite for the amplitude modulation to occur.

One important caveat, however, has to be taken into account. The mental rotation task with characters as stimuli suffers from an important confounding. Presentation of the rotated character not only involves the mental rotation process itself, but might also invoke processing of the difficulty of the rotation task. Unfortunately, both aspects are perfectly confounded. The greater the angular disparity from the upright, the more mental rotation has to be executed. At the same time, however, an additional relationship holds true: The greater the angular disparity from the upright, the more difficult the task at hand is. So one might argue that it is the processing of the difficulty information rather than the mental rotation process itself that causes the amplitude modulation. Ull-

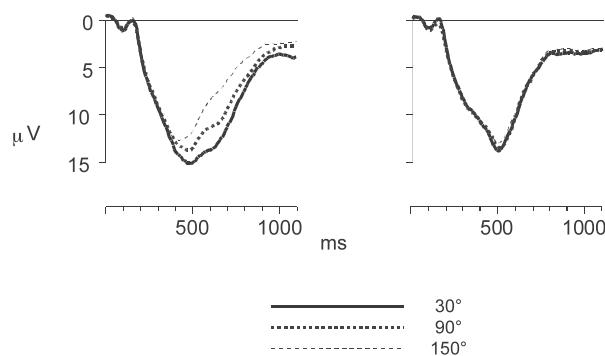


Figure 3. Grand average ERPs as a function of character orientation for go trials involving mental rotation (left) and nogo trials solved without mental rotation (right). See text for the description of the experimental procedure. Data from Heil et al. (1998).

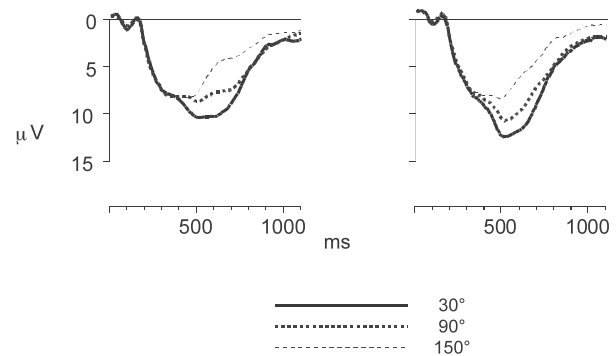


Figure 4. Grand average ERPs as a function of character orientation for go trials (left) and nogo trials (right) when both are involving mental rotation. See text for the description of the experimental procedure. Data from Heil et al. (1998).

sperger and Gille (1988), for example, found that the P300 amplitude evoked by a stimulus that signals the difficulty of a forthcoming task is related to the difficulty information conceived.

Therefore, the two aspects of mental rotation itself and processing of difficulty information, usually confounded, were separated in time in the study of Bajric, Rösler, Heil, and Hennighausen (1999). A visual cue was presented 3 s before the character for the mental rotation task. The cue—an arrow—provided valid information about the angular orientation of the character presented later. Therefore, the information about the difficulty of the task was given by the cue. Mental rotation itself, however, could not have been started before the character itself was presented. Thus, the two aspects were successfully separated in time.

The results (see Figure 5) clearly falsified the alternative explanation based on the difficulty information. The effects of the orientation of the cue and the orientation of the character differed according to their polarity (and also according to the topography; see Bajric et al., 1999). In fact, the amplitude of the P300 elicited by the cue was more positive when the cue signaled a more difficult task (i.e., nonupright pointing). Presentation of the character evoking mental rotation, however, elicited the well-known effects, that is, the potential was the more negative the more mental rotation had to be executed.

At least, these data show that the amplitude modulation was not evoked by the processing of the difficulty information but was closely linked to the process of mental rotation itself. The data do not prove that in a standard mental rotation task the two processes (mental rotation and processing of difficulty information) indeed do overlap. It might simply be the case that in the standard task processing of the difficulty information is not relevant. If, however, this aspect does also take place in the standard task, then, if anything, the effect size of the amplitude modulation is underestimated.

Irrespective of these details, however, the important point is that the alternative interpretation for the amplitude modulation was falsified by these data. At the moment, the process of mental rotation seems to be the most valid candidate in the search for the cause of the amplitude modulation. From an epistemological point of view, of course, it is impossible to positively prove the functional relationship between mental rotation and the amplitude modulation. The data presented so far, however, at least show that no empirical evidence exists against the functional relationship model. The predictions we tested so far based on the functional relationship model were verified.

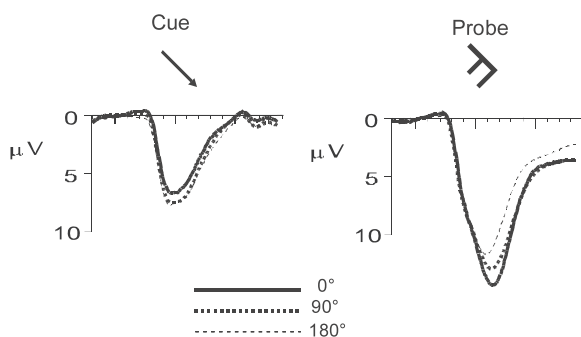


Figure 5. Grand average ERPs as a function of cue orientation (left) and character orientation (right). See text for the description of the experimental procedure. Data from Bajric et al. (1999).

The Temporal Relationship between Mental Rotation and the Amplitude Modulation

An additional strategy for examining the relationship between mental rotation and the amplitude modulation is to investigate the temporal aspects of the cognitive process (and its proposed electrophysiological correlate) in more detail. In doing so, it is possible to take advantage of the high temporal resolution event-related potentials do provide, a resolution that is not achieved by alternative brain imaging techniques like PET or fMRI providing a higher spatial resolution.

This second strain of research, therefore, reads as follows: Given that the amplitude modulation of the ERP due to character orientation directly reflects the process of mental rotation, then the onset of the amplitude modulation consequently should reflect the onset of the process itself. Moreover, an experimental manipulation prolonging information processing stages before mental rotation and, thus, postponing mental rotation itself should also postpone the onset of the amplitude modulation. Finally, experimental manipulations affecting the duration of processing stages involved after mental rotation has finished should have no effect whatsoever on the onset of the amplitude modulation.

According to traditional theories of mental rotation (e.g., Corballis, 1988; Shepard & Cooper, 1982), functionally independent information processing stages can be differentiated in a mental rotation task. These are (1) perceptual encoding, (2) identification/discrimination of the character and identification of its orientation, (3) mental rotation itself, (4) judgment of the parity, (5) response selection, and, (6) response execution. These stages are assumed to be organized sequentially with discrete information transmission from one stage to the next. The discrete and sequential nature of the model currently is under debate (see, e.g., Ruthruff & Miller, 1995; Stoffels, 1996). The empirical evidence from experimental psychology so far suggests that the processes are either organized in a strictly sequential manner (e.g., Stoffels, 1996), or that consecutive processing stages do overlap but only to a very small extent (e.g., Ruthruff & Miller, 1995). Given that this dichotomy is not the purpose of the present review, based on the empirical evidence available, the assumption seems quite valid that these subprocesses are executed successively.

That, of course, means that if the temporal relationship model is valid, then (a) the experimental manipulation of perceptual encoding should affect the onset of the amplitude modulation as should (b) the experimental manipulation of character identification/discrimination, whereas (c) the experimental manipulation of the parity judgment should have no effect.

We tested these predictions in a number of experiments. By comparing a high perceptual quality condition with a low one (less contrast and visual noise added), we (Heil & Rolke, 2002a, Experiment 1) manipulated the duration of perceptual encoding. This manipulation had an effect on response times of about 200 ms that was additive with the effect of orientation (see Figure 6), suggesting that the process of mental rotation was delayed in the case of a low perceptual quality because of a prolonged perceptual encoding.

Figure 6 also presents the amplitude modulation as the difference potential calculated by subtracting the 30° from the 150° condition.³ There is an amplitude effect present that was not predicted by the model that we will ignore for the moment and come back to at the end of this article. More important, there is clearly an onset-latency effect present: In the low perceptual qual-

³For the original waveforms, see Heil and Rolke (2002a).

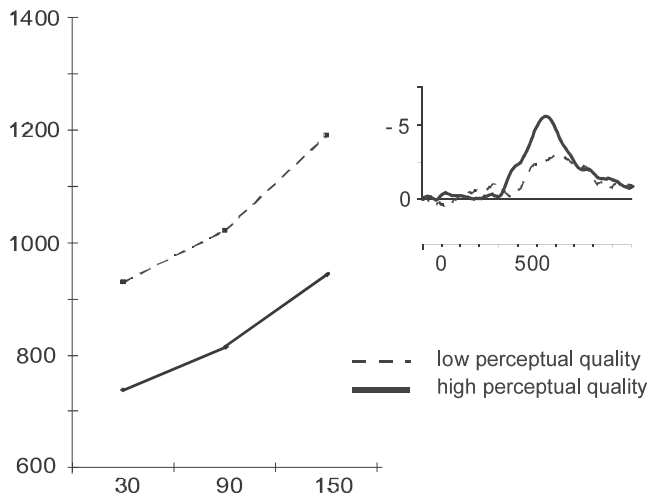


Figure 6. Left: Mean response times as a function of character orientation and perceptual quality. Right: Mental-rotation-related amplitude modulation (difference waveforms 150° minus 30°) as a function of perceptual quality. Data from Heil and Rolke (2002b).

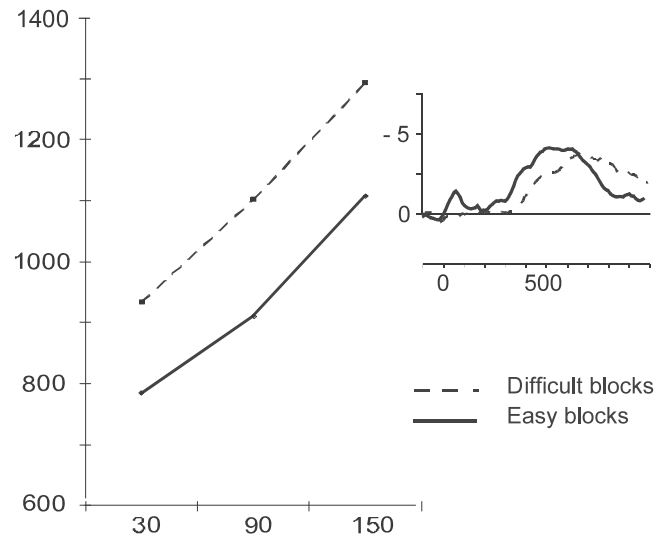


Figure 7. Left: Mean response times as a function of character orientation and discrimination difficulty. Right: Mental-rotation-related amplitude modulation (difference waveforms 150° minus 30°) as a function of discrimination difficulty. Data from Heil and Rolke (2002b).

ity condition, in which the onset of the cognitive process of mental rotation is delayed, the onset of the amplitude modulation is delayed, too. Moreover, the version of the character (normal versus mirror-reversed), affecting the duration of the parity judgment processing stage, had no effect whatsoever on the onset of the amplitude modulation. To sum up, this experiment provided the first empirical evidence for the temporal relationship between the cognitive process of mental rotation and the amplitude modulation in the ERP.

The same pattern of effects should also be found if the subsequent processing stage after perceptual processing but before mental rotation, that is, character identification and discrimination, is manipulated. For this end, we (Heil & Rolke, 2002a, Experiment 2) went back to an experimental manipulation originally introduced by Ruthruff and Miller (1995) with response times as dependent variables. In this experiment, four different characters (e, F, g, 7) were used for the parity judgment. In each of the four blocks, only one of two possible characters was presented in each given trial with the subject being aware of this manipulation. In the easy character discrimination blocks, the two characters used were very dissimilar and thus, easy to identify and discriminate (e.g., an e or an F). In the difficult character discrimination blocks, however, the mirror version of the one character was quite similar to the normal version of the other character used (e.g., an F and a 7).

Response times replicated the results of Ruthruff and Miller (1995); see Figure 7. The effect of character discrimination difficulty and orientation turned out to be additive, suggesting that this manipulation delayed the onset of mental rotation proper. In accordance with the temporal relationship model, the onset of the amplitude modulation was delayed if character discrimination was difficult (see Figure 7). Response times (RTs) for normal characters were some 150 ms shorter than RTs for mirror-reversed characters, an effect assumed to be due to a prolonged parity judgment stage (Shepard & Cooper, 1982). Nevertheless, the onset of the amplitude modulation was the same irrespective of the parity.

The two experiments reported so far validated the temporal relationship model. The onset of the amplitude modulation as a function of character orientation is delayed in time when the onset

of the mental rotation process is delayed due to a manipulation of either the perceptual encoding or the character classification and discrimination process. An experimental manipulation affecting the parity judgment process, however, does not affect the onset of the amplitude modulation at all, even if the RT effect turns out to be of comparable size.

The empirical evidence reported with respect to mental rotation in single-task situations, however, cannot be automatically generalized towards mental rotation in dual-task situations. Heil and Rolke (2002b), therefore, tested the validity of the temporal relationship model in dual-task situations in which a considerable amount of ERP component overlap occurs.

In this experiment, subjects were presented sequentially with a tone and a character with the stimulus onset asynchrony (SOA) manipulated (either 50 or 350 ms). The tone had to be classified as high or low in pitch by a button-press response. The task for the character (character classification vs. parity judgment), however, was dependent upon the tone classification. So, for example, for one subject, the instruction was if the tone is low then decide if the character is a letter or a digit; if the tone is high, however, decide whether the character is presented in normal or mirror-reversed format. The implications of this manipulation are straightforward: With the long SOA, subjects have time to classify the tone before the character pops up. Therefore, they should be able to go ahead with the task indicated by the tone with no delay. If the SOA is short, however, no information regarding which task is required is available when the character is presented. Therefore, subjects should postpone the processes involved in order to respond to the character (classification vs. mental rotation) until they know what task was indicated by the tone.

As a consequence of that, the processing delay induced by the SOA manipulation should be additive with the orientation effect if the tone indicates mental rotation. Moreover, an amplitude modulation as a function of character orientation should only be present if the tone indicates the mental rotation task. Finally, the amplitude modulation in the mental rotation task should be delayed if the SOA is short because the process of mental rotation is postponed.

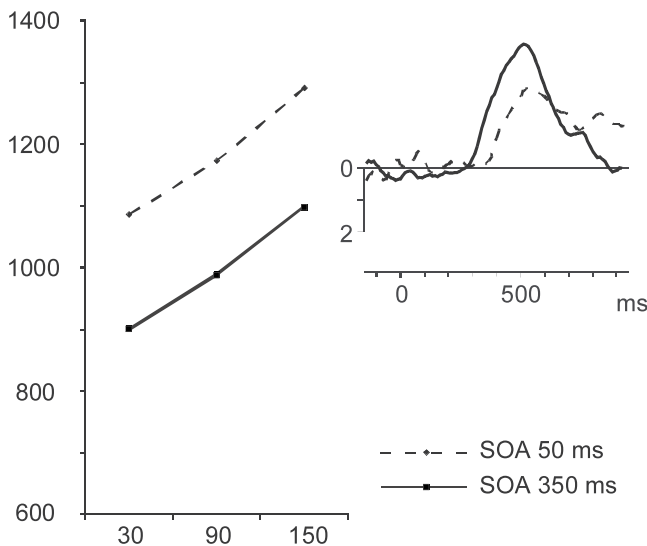


Figure 8. Left: Mean response times as a function of character orientation and SOA between the tone and the character in trials in which the tone indicated a parity judgment task. Right: Mental-rotation-related amplitude modulation (difference waveforms 150° minus 30°) as a function of SOA in the mental rotation condition. Data from Heil and Rolke (2002b).

Heil and Rolke (2002b) obtained exactly the data predicted above. If the tone indicated a character classification task, both RT and ERPs were independent of character orientation. If the tone, however, indicated a mental rotation task, RT revealed that the SOA effect and the orientation effect were additive (see Figure 8), suggesting that indeed the process of mental rotation was postponed if the SOA was short. The ERP data, in fact, validated this conclusion. The onset of the amplitude modulation was clearly delayed; see Figure 8. To sum up, these data show that the temporal relationship between mental rotation and the amplitude modulation does also hold in the case of dual-task situations in which multiple stimuli are presented in short succession evoking a considerable amount of ERP component overlap.

Therefore, the empirical evidence regarding the temporal relationship between mental rotation and the amplitude modulation so far is quite convincing. Whatever experimental manipulation was used to postpone the process of mental rotation (perceptual quality, difficulty of character classification, or SOA in a dual-task situation, respectively), the amplitude modulation was also postponed.⁴ At the same time, the difference between normal and mirror-reversed characters despite producing RT effects of about the same size had no effect on the onset of the amplitude modulation. From a theoretical point of view, this is what was expected, because this manipulation was supposed to have affected the duration of processing stages located after mental rotation was executed. To sum up, all these data suggest that the onset of the amplitude modulation as a function of the orientation of the character provides a

⁴The postponement in ERP onset latency was always smaller than the RT effect. This discrepancy, however, might be accounted for by methodological reasons. The RT-effect is based on the mean of the discrete, single-trial response times, and is thus affected equally by all responses. The ERP latency effect, in contrast, is based on the mean of the single-trial waveforms averaged. The onset of the ERP effect is therefore determined more by trials in the fast end of the RT distribution (see Meyer, Osman, Irwin, & Yantis, 1988).

chronopsychophysiological marker for the onset of mental rotation process proper.

Applying the Results to an Open Question in Experimental Psychology

In the following section, first the basic principles of the psychological refractory period (PRP) paradigm and the central bottleneck model (Pashler, 1994) are reported. Then, the contradictory RT data concerning mental rotation in the PRP paradigm are reviewed, with a possible theoretical solution originally suggested by Ruthruff, Miller, and Lachman (1995). Finally, recent ERP data (Heil, 2002) will be reported as the first empirical support for this theoretical claim.

The logic of the PRP paradigm reads as follows. The stimuli for two different tasks (S1 and S2) are presented in rapid succession with the interval between them (the SOA) varied. Participants are asked to respond to both stimuli as quickly as possible with the restriction (imposed in most but not all studies) that R1 should precede R2. Whereas RT1 proved to be (more or less) independent of SOA, decreasing SOA resulted in sharp increases of RT2 (the so-called SOA effect). Numerous studies using this paradigm have produced results that are more or less in line with the central bottleneck model (Pashler, 1994). According to this model, the chain of processing stages for each choice-reaction task can be divided into three successive classes of processing stages: (1) prebottleneck stages, such as preprocessing or feature extraction, (2) stages of information processing that do require access to the central bottleneck, such as response selection (see, e.g., McCann & Johnston, 1992) or short-term memory scanning (Heil, Wahl, & Herbst, 1999), and (3) postbottleneck stages, like program loading and motor adjustment. It is assumed that for any one task, this chain of processing stages is executed consecutively. In the case of dual-task performance, the central bottleneck model allows for any class of processing stages of Task 1 to occur in parallel with any class of processing stages of Task 2 with just one but important restriction: Processes that require the central bottleneck cannot occur in parallel!

There are important consequences of this processing model for the PRP paradigm (see Pashler, 1994, for a detailed account). Given the first task to be a simple high–low tone discrimination and the second task to be a visual discrimination task, let us first consider the case of a low task-overlap condition, that is, a long SOA. At some point after the tone had been presented (and thus, the processing chain for Task 1 has started), the visual stimulus is presented, and the chain of processing stages for Task 2 starts. At the time response selection (a central bottleneck process) of Task 2 is to begin, response selection of Task 1 is already finished—thus, the central bottleneck is available for Task 2, and can start working without interference from Task 1. Therefore, in the low overlap condition, RT2 is assumed to be equivalent to the RT in a single-task condition.

Next, let us consider the case of a high task-overlap condition, that is, a short SOA. Task 1 and Task 2 processing overlap temporally, with Task 1 processing assumed to be unaffected by Task 2 processing. Prebottleneck processes of Task 2 start as soon as S2 is presented, and they are assumed to be unaffected by Task 1 processing. However, as soon as response selection (or any other central bottleneck process) of Task 2 is attempted, a “cognitive slack time” is created. Bottleneck processes of Task 2 have to be postponed until after bottleneck processes of Task 1 are finished, and as a consequence, the SOA effect is created.

Given these assumptions to be valid, then the PRP paradigm can be used as a diagnostic tool to establish the locus of an experimental manipulation with respect to the central bottleneck, as suggested by Pashler (1994). If the effects of Task 2 manipulation and the SOA effect are additive, then the manipulation prolongs processes that require access to the central bottleneck.⁵ Because bottleneck processes of Task 2 have to wait until bottleneck processes of Task 1 are completed, the effect of the experimental manipulation is completely postponed until the end of the cognitive slack time.

If there is an underadditive interaction of these effects, however, then the process affected by the manipulation is to be located prior to the central bottleneck. If the process does not require access to the central bottleneck, the cognitive slack time can be used for this process, and as a consequence, the effect should be attenuated with increasing task overlap. In fact, the central bottleneck model allows the prediction of the amount of underadditivity, based on the cognitive slack time (estimated by the SOA effect) and probabilistic processing stage durations (see Ruthruff et al., 1995, for the model details).

In three recent studies (Heil et al., 1999; Ruthruff et al., 1995; Van Selst & Jolicoeur, 1994), tone discrimination was used as Task 1, and a character that was to be mentally rotated in order to judge its parity was used as S2. The critical question was whether mental rotation requires access to the central bottleneck. Ignoring minor methodological differences between the three studies as well as minor differences in the results, the situation is quite straightforward but theoretically puzzling: First of all, most of the experiments reported reliable underadditive interactions between the SOA effect and the orientation effect. The magnitude of the orientation effect is attenuated as the overlap between the tone discrimination and the mental rotation task is increased. Second, however, a very strong residual orientation effect remained present despite a large amount of cognitive slack time. In fact, the central bottleneck model would predict a much stronger attenuation of the orientation effect if mental rotation does not require access to the central bottleneck (see Ruthruff et al., 1995).

The first result excludes the possibility that mental rotation does require access to the central bottleneck, whereas the second result excludes the possibility that mental rotation does not require access to the central bottleneck. The model suggested by Pashler (1994), however, allows exactly for these two possibilities, both of which are to be rejected on the basis of the empirical data available.

This contradictory situation in experimental psychology has been obvious for a couple of years now (and is mentioned in all three papers), but no real solution has emerged yet. Van Selst and Jolicoeur (1994), for example, discuss the assumption of probability mixtures. For instance, it might be possible that some subjects can perform mental rotation without access to the central bottleneck whereas the majority cannot. Alternatively, it might be possible that all subjects can perform mental rotation without access to the central bottleneck, but they do so only on occasional trials. None of these probability mixture models is very appealing, however, and in fact, the empirical evidence shows no support for any of these models (e.g., Heil et al., 1999).

One solution for this contradiction was offered in the literature: Ruthruff et al. (1995) consider the possibility that there is not only

one orientation-dependent cognitive process involved in the mental rotation task but, actually, two. If one of these processes can be carried out without assistance from the bottleneck mechanism whereas the other cannot, then the former one could be responsible for the underadditivity whereas the latter one could be responsible for the very strong residual orientation effect at the shortest SOA (see also Ruthruff & Miller, 1995).

Because this idea definitely would perfectly predict the pattern of results, it is quite appealing. Unfortunately, however, I am not aware of any published independent empirical evidence for the assumption that there are two independent cognitive processes involved in the mental rotation process.⁶ Empirical support for this assumption could open the deadlock created by the experiments involving mental rotation in the PRP paradigm (Heil et al., 1999; Ruthruff et al., 1995; Van Selst & Jolicoeur, 1994). This, in turn, would create the possibility for ending a very unsatisfying situation, in which researchers simply agree that they cannot really explain a reliable pattern of results.

Therefore, we (Heil, 2002) recorded the mental-rotation-related amplitude modulation in the PRP paradigm. On each trial, participants first made a speeded response classifying a tone as high or low and afterward judged a character as being presented normal or mirror-reversed by a second key-press response. The SOA between the tone and the character was either 50 ms, 200 ms, or 350 ms. Additionally, in a quarter of the trials, no character was presented at all after the tone in order to prevent response grouping (see, e.g., Pashler, 1994).

Response times replicated our previous results (Heil et al., 1999). RT1 was more or less independent of SOA. RT2, however, increased as a function of character orientation and was the longer the shorter the SOA (see Figure 9).⁷ Close inspection of Figure 9 will eventually also reveal the small but reliable underadditive interaction between SOA and character orientation. Again, the underadditivity observed turned out to be much smaller than predicted by the central bottleneck model. The onset of the mental-rotation-related negativity expressed as the difference potential between the 150° and the 30° condition, however, was completely independent of the SOA. That is, whatever the SOA, the amplitude modulation starts at the very same time.

We want to stress, at this point, the similarity between the dual-task study reported earlier (Heil & Rolke, 2002b) and the PRP study (Heil, 2002). The former one, however, relied on a strategic postponement of the process of mental rotation. In the short SOA condition, subjects simply do not know whether they are asked to do mental rotation or character classification, and as a consequence of that, they most probably postpone all the processes related to mental rotation until they know for sure that this is the task required. In the PRP paradigm, however, subjects know for sure that they are required to mentally rotate the character. According to Pashler (1994), the response times reveal the consequences of a supposedly structural postponement due to processing limitations imposed by the central bottleneck that is unavoidable by the system (see Pashler, 1994). However, the strategic postponement resulted in a delay in the onset of the mental-rotation-related amplitude modulation, whereas the structural one did not.

⁶Some authors (e.g., Ruthruff et al., 1995) argue that character identification times are orientation dependent. The empirical evidence, however, clearly contradicts this claim; see, for example, Heil et al. (1996).

⁷In PRP experiments, RT data are regularly shown in graphs with SOA presented at the abscissa. This habit was violated in Figure 9 in order to realize a coherent presentation of the results.

⁵Theoretically, it is also possible in this case that the experimental manipulation prolongs processes located after the central bottleneck; see Pashler (1994). This possibility, however, is of no relevance for the experimental situations described in this article.

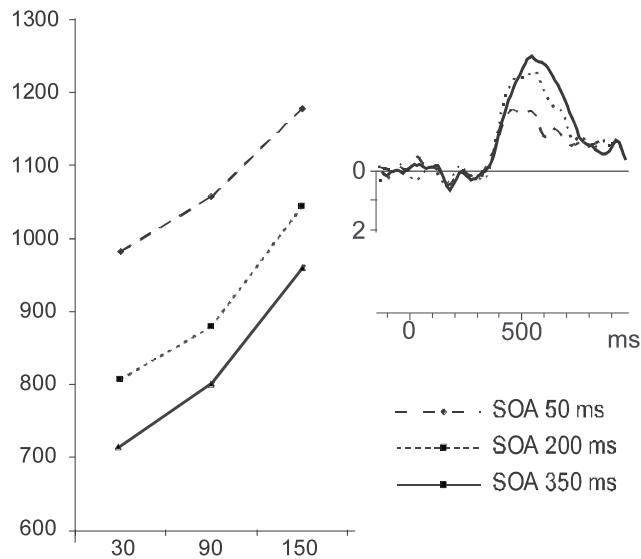


Figure 9. Left: Mean response times as a function of character orientation and SOA between tone and character in a PRP experiment. Right: Mental-rotation-related amplitude modulation (difference waveforms 150° minus 30°) as a function of SOA. Data from Heil (2002).

We are, actually, far from postulating that these data do finally solve the problem presented above. But they are definitely a way forward on this approach. It is still perfectly possible that the whole central bottleneck model (Pashler, 1994) simply is wrong (see, e.g., Heil et al., 1999; Hommel, 1998; Meyer & Kieras, 1997a, 1997b), and an alternative model might be able to explain the data (despite the fact that it has not been proposed yet). In regards to the alternative assumption put forward by Ruthruff et al. (1995), however, these findings for the first time at least point towards a strategy of experimental investigation.

Let us assume for a moment that Ruthruff et al. (1995) are indeed correct in claiming that there are two orientation-dependent processes involved in mental rotation, the first one working without access to the central bottleneck and the second one requiring access. The RT data, then, suggest that the first process causes the underadditivity, whereas the second is responsible for the strong residual orientation effect. The ERP data, now, would suggest that the amplitude modulation is an electrophysiological correlate of the first process, whereas the second is not reflected in the amplitude modulation. Still, we do not know what these two processes are in detail,⁸ but if they do exist, then at least we do know how to validate whether the first one is present in a certain task. Or, from a different point of view, the experiments aimed at identifying the relationship between mental rotation and the rotation related amplitude modulation might benefit from a new momentum: The search for the hypothesized two orientation-dependent cognitive processes. That is, an experimental approach that was firmly based

⁸More recent theories (e.g., Farah, 1995; Kosslyn, Maljkovic, Hamilton, Horowitz, & Thompson, 1995) broke down the mental rotation process into different subprocesses. It is assumed that while the image is actually rotated, control processes inspect and compare the transformed image. These subprocesses are either assumed to occur in parallel, or in an iterative chain (i.e., rotate, compare, rotate, compare, rotate, etc.). Much more empirical evidence is needed, however, before these new models can be applied to the problem ahead.

in psychophysiology, now, we hope, moves more towards experimental psychology, a change from which both sides can (and, we hope, will) benefit.

Further Issues with Respect to the Electrophysiological Correlates of Mental Rotation

The review presented here has focused on the functional as well as the temporal relationship between mental rotation and the orientation-dependent amplitude modulation. As a consequence, a number of important issues were ignored throughout the article, and should at least be mentioned here.

Amplitude Effects in the Temporal Relationship Studies

In some of the studies (see above) investigating the temporal relationship between the process of mental rotation and the onset of the amplitude modulation, we obtained an unpredicted reduction of the amplitude of the ERP modulation in those conditions in which mental rotation was postponed. Some of this reduction might be accounted for by methodological reasons. It is well known that an increase in RT is accompanied by an increase in the standard deviation of RT. This increase might result in some smearing of the peak amplitude of the ERP effect. This would also explain (at least in part) why the RT effect in these studies was larger than the latency effect in the ERP (see also footnote 4). It is still an open question, however, whether methodological reasons can fully account for the unpredicted amplitude effects. The empirical evidence available so far, however, does not really justify theoretical reasons as an alternative. Some data suggest that information processing in a mental rotation task should not be understood as being organized sequentially with discrete information transmission (see below). More experiments are needed to see whether the supposedly nonsequential organization of information processing can account for the amplitude effects.

The Topography of the Effect and the Brain Structures Involved

In all studies using ERPs, the orientation-dependent amplitude modulation showed its maximum at parietal electrode leads. Although there is some support for the notion that mental rotation should be understood as a right parietal dominant function (e.g., Bajric et al., 1999; Yoshino, Inoue, & Suzuki, 2000), the majority of the papers published, however, suggest a bilateral cortical involvement (e.g., Heil et al., 1996; Heil, Rauch, & Hennighausen, 1998; Heil & Rolke, 2002a; Rösler, Heil, Bajric, Pauls, & Hennighausen, 1995). This result fits perfectly with studies using fMRI demonstrating bilateral cortical activation in the superior and inferior parietal lobe (see, e.g., Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Richter et al., 2000).

Effects of Stimulus Complexity and Type of Task

An interesting but still unresolved question is whether the complexity of the stimulus and/or the type of the mental rotation task affects “only” the difficulty of the process, or whether it might introduce qualitative changes in the cognitive process(es) involved. The question cannot only be addressed from a purely behavioral point of view (see, e.g., Bethell-Fox & Shepard, 1988; Shepard & Metzler, 1988), but also from a psychophysiological one. By using fMRI, Jordan et al. (2001) showed that more or less the same brain areas were involved during the mental rotation of three-dimensional-block figures similar to those used by Shepard and Metzler (1971), of letters, and of two-

dimensional abstract figures, respectively. Rösler, Heil, Bajric, Pauls, and Hennighausen (1995) used a mental rotation task with abstract two-dimensional figures in which participants had to rotate an image on command of an instruction stimulus. Participants inspected a starlike figure constructed from 12 black and white triangles. Then the stimulus was withdrawn. On command of an instruction stimulus, the memorized image had to be maintained for 9 s, to be rotated for 60°, or to be rotated for 120°. The transformed image was then compared with a test stimulus. In this situation, a very pronounced, long-lasting negativity appeared over the parietal cortex. Its amplitude increased with increasing rotational angle. A tactile version of the task (see Röder, Rösler, & Hennighausen, 1997) yielded the same topographic pattern of effects, that is, an increase in negativity with increasing rotational angle at parietal electrode leads (Rösler, Röder, Bajric, & Heil, 1995). These results, however, do not yet provide strong evidence as to whether the more phasic amplitude modulation reported in this review and the slow negativity observed by Rösler, Röder, et al. (1995) are generated by the same and only the same cortical tissue and/or the same and only the same cognitive process(es).

Individual Differences in the Mental Rotation Abilities

Mental rotation is one of the most important tasks to measure spatial intelligence, and, in fact, most of the gender differences in spatial abilities have to be traced back to gender differences in speed and accuracy of mental rotation (see, e.g., Voyer, Voyer, & Bryden, 1995). Unfortunately, the relationship between individual differences in spatial abilities and their neuronal correlates are still very poorly understood (see, e.g., Willerman, Schultz, Rutledge, & Bigler, 1992). Rösler, Heil, Pauls, Bajric, and Hennighausen (1994) divided a larger sample of participants into two groups according to their spatial intelligence scores, and found group differences over left but not over right parietal electrode leads. Although these data fit nicely in Kosslyn's (1987) theoretical framework of mental imagery, much more work needs to be done on this issue. To make things even more complicated, this work has to take into account the effects of practice on mental rotation (see, e.g., Heil, Rösler, Link, & Bajric, 1998).

Spatial Transformation versus Action Planning

The involvement of the parietal cortex in mental rotation and the fact that mental rotation is one of the most widely used tasks to measure spatial abilities might, probably, make perfect sense for most readers. Mental rotation is understood as a task of spatial transformation, and spatial processing is believed to take place in the parietal cortex (see, e.g., Heilman & Valenstein, 1993). Based on this chain of reasoning, the finding of Heil, Rösler, et al. (1998) fit into the overall picture. By combining a spatial versus a verbal long-term memory retrieval task with a gender classification task for words versus a mental rotation task, the authors obtained a clear-cut double dissociation. The gender classification task interfered much more strongly with verbal than with spatial memory retrieval. More relevant, mental rotation interfered much more strongly with spatial than with verbal memory retrieval.

Recently, however, the view of mental rotation as a spatial task located in the parietal cortex was challenged by an alternative view. Wexler, Kosslyn, and Berthoz (1998) and Wohlschläger and Wohlschläger (1998) argue that mental rotation heavily relies on motor processes. Some of the brain imaging studies using fMRI indeed found activation in the motor cortex (e.g., Cohen et al., 1996) for at least some of the participants whereas others did not

(Jordan et al., 2001). Wexler et al. (1998) and Wohlschläger and Wohlschläger (1998), however, based their argument on an observed interference between mental and manual rotation. The exact level of this interference, however, is still poorly understood (see Heil, Rolke, and Hennighausen, 2002), and much more work is needed to examine the role of motor processes in mental rotation in more detail.

Response Preparation during Mental Rotation?

Finally, to complete the list of poorly understood aspects of mental rotation from a psychophysiological point of view, one has to mention the debate as to whether response preparation can proceed during mental rotation or not. According to discrete serial stage models of information processing (e.g., Sanders, 1980; Sternberg, 1969), this should not be possible, whereas alternative models (e.g., Eriksen & Shultz, 1979; McClelland, 1979; Miller, 1988) explicitly allow for this possibility. Theoretically, the two-alternative forced-choice go-nogo task in combination with the lateralized readiness potential (LRP; see, e.g., Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992; Smid, Mulder, Mulder, & Brands, 1992) provides the ideal approach to solve this dispute. Therefore, Band and Miller (1997) presented rotated characters for the mental rotation task in different colors. The color determined the responding hand (left or right) whereas the parity of the character (normal vs. mirror-reversed) determined whether the response had to be executed or withheld. Because the color classification could be done much faster than the parity judgment, the LRP should provide evidence for response preparation during mental rotation, if and only if this parallel processing is possible but not if a discrete serial stage model is valid. Band and Miller (1997), in fact, obtained (almost) no LRP activity at all during mental rotation and therefore concluded that response preparation is absent during mental rotation (see also Stoffels, 1996).

In our two-alternative forced-choice go-nogo study (Heil, Rauch, & Hennighausen, 1998) described in detail above, we also recorded the LRP, and, in fact, obtained clear-cut evidence for response-hand preparation during mental rotation. The contrary results of Band and Miller (1997) and of Heil, Rauch, and Hennighausen (1998) may be caused by the way the easy decision determining the responding hand was realized. In our study, letter versus digit classification was used. Because it is generally assumed (e.g., Jolicoeur & Cavanagh, 1992) that character identification is done before mental rotation, the information regarding the response hand can be seen as an obligatory by-product of the information processing that is needed for mental rotation. Thus, even if participants exclusively rely on mental rotation, the information for response-hand preparation is present and, probably as a consequence, is actually used.

In the Band and Miller (1997) study, however, the responding hand was determined by the color of the character, and thus, the situation might be different. Mental rotation obviously *can* begin without analyzing the color. Thus, in this study, the information for response-hand preparation is optional, and probably, therefore, participants might adopt a different strategy.

Although this explanation is quite speculative, the distinction between—on the one hand—obligatory information that is present in and indeed used by the system and—on the other hand—optional information that is not used might over and above the question of mental rotation have potential impact on mental chronometry as such. Again, as with the other issues mentioned, further studies are strongly needed (see, e.g., Heil, Hennighausen, & Özcan, 1999).

Summary and Conclusion

In a parity judgment task, the ERPs at parietal electrode sites become the more negative the more mental rotation has to be executed. It was claimed (Wijers et al., 1989) that this amplitude modulation should be understood as an electrophysiological correlate of the mental rotation process itself. This article presented the recent experimental investigations of this plausible although speculative hypothesis that can be summarized as follows:

- Classification of disoriented characters that can be done without mental rotation does not evoke the amplitude modulation.
- In a parity judgment task that involves mental rotation, the amplitude modulation is present irrespective of whether a manual response had to be executed or withheld.
- Processing of the orientation of the stimulus (and thus, of the difficulty of the task) does not evoke the amplitude modulation. Moreover, the amplitude modulation also is present in experimental situations where subjects know the orientation of the character before the character is presented.
- If the perceptual quality of the character is reduced, the process of mental rotation is postponed. At the same time, the amplitude modulation is delayed.
- If the difficulty of character identification is increased, the pro-

cess of mental rotation is postponed. At the same time, the amplitude modulation is delayed.

- In a dual-task situation in which subjects strategically postpone the process of mental rotation, the amplitude modulation also is delayed.

All these results confirm the hypothesis originally proposed by Wijers et al. (1989) regarding the functional significance of the amplitude modulation obtained in mental rotation tasks. The amplitude modulation might indeed be a direct electrophysiological correlate of mental rotation. This most plausible hypothesis was confirmed by experiments addressing both the functional and the temporal relationship between mental rotation and the amplitude modulation.

Applied to the PRP paradigm, the ERP results in themselves do not solve the theoretically important problem outlined above. They do, however, point towards a cooperative strategy from which both experimental psychology and cognitive psychophysiology might profit. It is the author's strong belief that this holds true for most of the unresolved issues described in detail above. The range of areas that would benefit from experimental research into these issues, however, would definitely include more disciplines, like neuroscience, spatial intelligence, individual differences, mental chronometry, or motor processes. Despite more than 30 years of research into mental rotation, there still exist many things we simply do not yet understand.

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