Event-related brain potentials and cognitive processes related to perceptual–motor information transmission

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In the present study, event-related potentials (ERPs) were recorded to investigate cognitive processes related to the partial transmission of information from stimulus recognition to response preparation. Participants classified two-dimensional visual stimuli with dimensions size and form. One feature combination was designated as the go-target, whereas the other three feature combinations served as no-go distractors. Size discriminability was manipulated across three experimental conditions. N2c and P3a amplitudes were enhanced in response to those distractors that shared the feature from the faster dimension with the target. Moreover, N2c and P3a amplitudes showed a crossover effect: Size distractors evoked more pronounced ERPs under high size discriminability, but form distractors elicited enhanced ERPs under low size discriminability. These results suggest that partial perceptual–motor transmission of information is accompanied by acts of cognitive control and by shifts of attention between the sources of conflicting information. Selection negativity findings imply adaptive allocation of visual feature-based attention across the two stimulus dimensions.

The present study was conducted in order to assess the dynamics of the availability of partial information from different types of preliminary perceptual processing. Visual perception of object features, for example, is a highly modular process that implies some form of independent and parallel processing of basic features (e.g., color, shape, size, motion; see, e.g., Livingstone & Hubel, 1988) that are fragmented and registered in specialized visual areas of the cortex (e.g., Van Essen, Anderson, & Felleman, 1992). The transmission of modular information in visual-to-motor pathways has remained a relatively neglected issue, although the modularity of the visual system is a highly investigated topic in current cognitive neuroscience. In the present article, we describe an experiment that was designed to investigate feature-specific visual-to-motor transmission of information.

Whether response preparation can begin before stimulus recognition is complete is important for discriminating between discrete and continuous models of information processing (Miller, 1988; Sanders, 1990): Although discrete models deny the possibility of such response preparation, continuous models affirm this possibility. Discrete information-processing models assume that a mental process must finish before a subsequent mental process can begin, so that different processes operate in a strict, sequential manner (Sternberg, 1969). This assumption has been criticized by a number of researchers who have argued that a given mental process need not finish com-

pletely before the next process begins. Several continuous information-processing models have been proposed (see, e.g., Eriksen & Schultz, 1979; McClelland, 1979). Continuous models assume that a process can transmit preliminary or partial output before it is completely finished. Subsequent processes can use preliminary output to begin working before the previous process has completely finished.

Miller (1982, 1983) suggested that a binary distinction between discrete and continuous models may be an oversimplification, and that it is possible to regard discrete and continuous models as two ends of a continuum. The continuum is defined by the size of the units (i.e., the “grain” size) of information transmission. Discrete models allow the transmission of information only about the stimulus as a whole, so response preparation cannot begin until the stimulus as a whole has been completely recognized. Continuous models allow transmission of indefinitely small units of information, so response preparation can begin as soon as any information about the stimulus becomes available. Intermediate models assume transmission of information grains that are neither arbitrarily small nor as large as the stimulus. Miller (1982, 1983) proposed an intermediate model of perceptual–motor transmission of information—the asynchronous discrete coding (ADC) model—in which response preparation can begin only after recognition processes have activated a code (Posner, 1978) used in categorizing a stimulus.

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Miller (1982, 1983) used stimulus sets in his experiments in which some stimulus information was available from a preliminary perceptual analysis (preliminary information) and other stimulus information was available only after more complete perceptual analysis (secondary information). The discriminability of secondary information was manipulated to vary the opportunity for preparing responses based on information extracted by the preliminary perceptual analysis, with more difficult secondary discriminations providing more time for preparation of responses using preliminary information. A similar logic was used in the present experiment (see below). Unlike in Miller's (1982, 1983) experiments, however, various components of the event-related brain potential (ERP) were assessed. The ERP technique offers measures of cortical activity with excellent temporal resolution, even if events do not require behavioral responses (Luck, 2005).

The nature of transmission of information from stimulus recognition to response preparation is a central issue in mental chronometry (Miller, 1988; Sanders, 1990) and in cognitive electrophysiology (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Coles, Smid, Scheffers, & Otten, 1995; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). Our present experiment parallels closely the study by Osman, Coles, Donchin, Bashore, and Meyer (1992). Osman et al. used stimuli with attributes of location and form (letter vs. number) and manipulated form discriminability. They measured lateralized readiness potentials (LRPs)—a direct measure of cortical response preparation (Coles, 1989; Kutas & Donchin, 1980). The LRP data showed that participants began to prepare responses based on the easy dimension (location), and that they terminated the preparation at different times, depending on when information from the form dimension became available, indicating that both stimulus attributes were processed simultaneously rather than in a serial manner. Another important complement of our study assessed perceptual-motor transmission of stimulus information in a choice reaction task with no-go trials (Miller & Hackley, 1992). When stimuli varied in shape and size, LRPs in no-go trials suggested that easily recognized shape information initiated response preparation and that this preparation was aborted when size analysis signified that the response should be withheld, contrary to assumptions of discrete models of perceptual-motor information transmission. When stimuli varied only in size, no evidence for preliminary response preparation was obtained, contrary to continuous models of perceptual-motor information transmission. Overall, the available LRP findings clearly suggest that response preparation can result from partial perceptual stimulus analysis in a manner that is consistent with ADC models of perceptual-motor information transmission (Miller, 1982, 1983).

Measuring multiple ERP components could be useful in elucidating additional details on cognitive processes that are related to perceptual-motor transmission of stimulus information. One of the best-described ERP components is the P3b, which is a parietal positivity, peaking at approximately 400 msec after stimulus onset. It is larger to infrequent stimuli, particularly when these stimuli are targets

in choice-response tasks (Kopp, 2008). There are two additional families of earlier ERP components that also show enhanced amplitudes in response to target stimuli in this kind of task. First, feature-based attention as assessed by ERPs affects processing in visual cortical areas (Hillyard & Anllo-Vento, 1998). This modulation, termed *selection negativity* (SN), was found for a variety of visual features, including color, shape, and spatial frequency. The SN is observed over the parieto-occipital scalp, beginning at around 150 msec and lasting 200 msec or more (Hillyard, Teder-Sälejärvi, & Münte, 1998). The cortical sources of the SN are probably located in the corresponding feature-selective areas of the extrastriate cortex (Schoenfeld et al., 2007). Second, a prefrontal positivity at about the same latency was described, termed P2a (Potts & Tucker, 2001), which is enhanced to visual target stimuli (Potts, 2004). There is little evidence regarding which cognitive process the P2a reflects (see, e.g., Luck & Hillyard, 1994), but it has been proposed that the P2a reflects stimulus evaluation in the service of task demands—that is, an early, perhaps preliminary, target-identification mechanism (Kopp, Tabeing, Moschner, & Wessel, 2007; Potts, 2004).

Distinct distractor-contingent components have also been described in various studies. First, infrequent stimuli that are irrelevant to the task (distractors), but that are more salient than the targets, evoke the P3a (Squires, Squires, & Hillyard, 1975), which peaks earlier and has a more frontocentral scalp distribution than the P3b. The P3a was conceived as a correlate of attentional orienting to salient distractors (Friedman, Cycowicz, & Gaeta, 2001). Second, stimulus displays containing response-incompatible distractors, as in flanker, Stroop, or certain go/no-go tasks, elicit an anterior N2, here termed N2c, which has a midline frontal scalp distribution and peaks around 250–300 msec poststimulus in tasks that utilize simple stimuli (Folstein & Van Petten, 2008; Kopp, Mattler, Goertz, & Rist, 1996; Kopp, Rist, & Mattler, 1996). The N2c amplitude is related to the degree of response conflict in choice reaction tasks. We proposed that the N2c may reflect the detection and suppression of to-be-inhibited responses (Kopp, Mattler, et al., 1996; Kopp, Rist, & Mattler, 1996). Other researchers have suggested that the anterior N2 is related to mechanisms that are required to dissolve decision conflicts (Yeung, Botvinick, & Cohen, 2004).

The aim of the present study was to explore additional details on cognitive processes related to perceptual-motor transmission of information by measuring multiple ERP components. Specifically, the N2c can be measured as an index of whether or not the occurrence of conflicts between preliminary and secondary information involves acts of cognitive control. A similar argument can be made with regard to the P3a as an index of shifts of attention between preliminary and secondary stimulus information when the two sources of information are in conflict with each other. Measuring the SN could provide additional information about whether or not attentional priorities are adaptively changed when the discriminability of one source of information is manipulated in such a way that the formerly preliminary information now becomes the secondary information, and vice versa.

In the present study, subjects classified two-dimensional visual stimuli with dimensions of size (large, small) and form (rectangle, ellipse). Each of the four feature combinations appeared equiprobably, with one of the four designated as the target (the stimulus consisting of the target-compatible size feature and the target-compatible form feature, $S+F+$) that required a buttonpress response (go trials—e.g., response to the small rectangles). The other three feature combinations were nontargets requiring no response (no-go trials—i.e., small ellipses, $S+F-$; large rectangles, $S-F+$; large ellipses, $S-F-$). Of particular interest were those distractors that shared one, but not the other, feature with the target (i.e., $S+F-$ and $S-F+$). The basic prediction was that these nontargets would elicit response conflict or the need to inhibit the prepared response (see below) and larger N2c and P3a amplitudes (see above) in the ERPs as compared with nontargets that shared no feature with the target ($S-F-$).

One could ask for a logical argument for the application of ERP amplitude measures. We outlined above that the N2c and P3a amplitudes are a function of preliminary response preparation. If there is no opportunity for preparing responses (as in the $S-F-$ trials), the amplitudes of these two ERP components can be considered as representing a baseline. The N2c and P3a amplitude enhancements (as compared with the baseline) in the $S+F-$ and $S-F+$ trials, respectively, serve to indicate to what magnitude preliminary response preparation takes place.

Our basic idea is that different stimulus dimensions can be processed independently (Cohen & Shoup, 1997) and in parallel (Rousselet, Thorpe, & Fabre-Thorpe, 2004), and that it eventually might take different amounts of time for completing these evaluations. We propose, in line with the assumptions that are made within the ADC model of information transmission from stimulus recognition to response preparation (Miller, 1982, 1983), that a need to inhibit the primed response will arise when the faster evaluation process results in identifying a target-compatible feature and when the slower process results in a target-incompatible feature. We further predict that this type of response conflict or inhibition of a prepared response should be identifiable in ERPs. Specifically, whenever the processing of a target-compatible feature (e.g., $S+$) terminates before the processing of a target-incompatible feature (e.g., $F-$), enhanced amplitudes of the N2c and P3a components are expected because an opportunity for response preparation based on preliminary information is given under these circumstances. We refer to this prediction as the *enhancement* prediction throughout the present article.

In an attempt to further test these ideas, the relative speed of processing between the two features (size and form) was manipulated by changing the difference between $S+$ and $S-$. Specifically, size discriminability was manipulated so that large and small shapes were quite different in one experimental condition, moderately different in another condition, and only slightly different in the low-discriminability condition. A smaller size difference is assumed to increase the decision time for size discriminations and thus for determining the presence of $S-$. The

manipulation of the relative speed of processing eventually leads to the reversal of the order of the completion of the evaluation processes. Under these circumstances, a crossover effect should be identifiable in ERPs. Critically, response conflict or the inhibition of a prepared response would arise only when the target-compatible feature is easier to detect than the target-incompatible feature. Size-compatible, form-incompatible ($S+F-$) nontargets would be quickly identified as possible targets when size is highly discriminable, and would thus elicit ERP signs of response conflict or inhibition of a prepared response. In contrast, when large and small are difficult to discriminate, stimulus form would eventually be identified first, and it would eventually be the size-incompatible, form-compatible ($S-F+$) nontargets that would elicit the largest N2c/P3a responses. We refer to this prediction as the *crossover* prediction throughout this article.

METHOD

Participants

Twenty-four volunteers participated ($M = 24$ years; range = 18–36 years; 11 males; 22 were right-handed).¹ All of the participants were unmedicated and neurologically unimpaired. All had normal or corrected-to-normal vision and normal hearing. Participants were either students at the University of Technology at Braunschweig or they were employees of the Klinikum Braunschweig. They were compensated with either course credits or payment (€15). A written-consent statement was obtained from participants after the nature and objectives of the experiment were explained.

Task Design

Figure 1 presents the stimuli that were used in the visuomotor decision-making task. A particular stimulus had two features (its size, large [l] or small [s], and its form, rectangle or ellipse). The four stimuli were produced by factorially combining the two levels of the two features.

Stimuli were presented one at a time in the center of a computer screen (FlexScan T766 19-in. [Eizo, Hakusan, Ishikawa, Japan]; $1,280 \times 1,024$ pixels at a 100-Hz presentation rate; a 100-msec stimulus duration; a 1,150-msec interstimulus interval). The viewing distance amounted to 1.25 m. Stimuli were displayed on a white background that extended over the complete computer screen. The stimulus presentation was controlled by the Presentation software (Neurobehavioral Systems, Albany, CA) that was installed on an IBM-compatible personal computer.

Participants were instructed that one stimulus was the target (denoted $S+F+$; i.e., the stimulus with the target size and with the target form) throughout the experiment. In any given trial, one out of the four stimuli was presented, and participants had to decide whether or not the current stimulus equaled the target. Participants pressed the space bar on a standard computer keyboard when the target had been recognized (handled by the right index finger). No response had to be emitted if the stimulus was recognized as one of the distractors. No feedback about response accuracy was provided.

There were three types of distractors: the size-overlap distractor ($S+F-$; i.e., the stimulus with the target-compatible size and with the target-incompatible form), the form-overlap distractor ($S-F+$; i.e., the stimulus with the target-incompatible size but with the target-compatible form), and the standard distractor ($S-F-$; i.e., the stimulus with the target-incompatible size and the target-incompatible form). Figure 1A depicts an example: When the large rectangle was the target stimulus, $S+F+$, the large ellipse was the size-overlap distractor, $S+F-$, the small rectangle was the form-overlap distractor, $S-F+$, and the small ellipse was the standard distractor, $S-F-$. Individual participants received different stimuli as

Figure 1. The stimuli were counterbalanced across participants. Columns show targets (leftmost column), size distractors (second column), form distractors (third column), and standard distractors (rightmost column). Rows show the four possible ways to define a particular stimulus set: (A) When the target (S+F+) equals the large rectangle, the large ellipse serves as a size (S+F-) distractor, the small rectangle as a form (S-F+) distractor, and the small ellipse as a standard (S-F-) distractor. (B) When the target equals the small rectangle, the small ellipse serves as a size distractor, the large rectangle as a form distractor, and the large ellipse as a standard distractor. (C) When the target equals the large ellipse, the large rectangle serves as a size distractor, the small ellipse as a form distractor, and the small rectangle as a standard distractor. (D) When the target equals the small ellipse, the small rectangle serves as a size distractor, the large ellipse as a form distractor, and the large rectangle as a standard distractor.

the target stimulus—that is, the large rectangle, the small rectangle, the large ellipse, or the small ellipse. Adequate counterbalancing (i.e., 6 participants received the large rectangle as the target; another 6 participants received the small rectangle as the target, etc.) thus yielded distractor types that were, on average, composed of physically identical stimuli. Thus, comparisons between averaged ERPs in response to the various distractor types avoid physical stimulus confounds (Luck, 2005).

The perceptual discriminability of the size of the stimuli was manipulated at three levels. This was accomplished by varying the spatial extension of the objects. The maximum size of the objects (rectangles, ellipses) amounted to 4.0° of visual angle (width) $\times$ 3.1° (height) for large objects, versus 1.4° (width) $\times$ 1.1° (height) for small objects, in the high-discriminability condition. In the medium-discriminability condition, the maximum size of the objects was 3.2° (width) $\times$ 2.6° (height) for large objects, versus 1.7° (width) $\times$ 1.3° (height) for small objects. Finally, large objects measured 2.6° (width) $\times$ 2.0° (height), whereas small objects measured 2.1° (width) $\times$ 1.6° (height) in the low-discriminability condition.

Each participant performed six blocks of 192 trials each ($6 \times 192 = 1,152$ trials overall). Blocks were divided by short breaks (lasting 2 or 3 min). The various stimulus types (i.e., S+F+, S+F-, S-F+, or S-F-) occurred equiprobably within blocks (in $192/4 = 48$ trials each). The order of succession of the stimulus types was random. Size discriminability was manipulated blockwise. The level of size discriminability was maintained across two consecutive blocks. Thus, within each level of size discriminability, each stimulus type occurred in $96 (2 \times 48)$ trials. The order of succession of the three levels of size discriminability (low, medium, high) was counterbalanced across participants.

Participants were instructed that they would receive four stimuli in rapid sequence, and that one stimulus would be the target (e.g., the “large rectangle”). They were informed about the randomness

of the stimulus sequence, and they were asked to respond as fast as possible without committing errors. Participants received 24 practice trials in the run-up to the experiment. The target detection task that was performed on the practice stimuli was based on the number (one or two) and the spatial orientation (toward the left or toward the right) of the green bars.

Electrophysiology

Continuous EEG was recorded by means of another IBM-compatible personal computer, a QuickAmps-72 amplifier (Brain Products, Gilching, Germany), and the BrainVisionRecorder software (Brain Products, Gilching, Germany) from frontal (F7, F3, Fz, F4, F8), central (T7, C3, Cz, C4, T8), parietal (P7, P3, Pz, P4, P8), occipital (O1, O2), and mastoid (M1, M2) sites. Ag-AgCl EEG electrodes were used. They were mounted on an EasyCap (EasyCap, Herrsching-Breitbrunn, Germany). Electrode impedance was kept below $10 \text{ k}\Omega$. All EEG electrodes were referenced to average reference. Participants were informed about the problem of noncerebral artifacts, and they were encouraged to reduce them (Picton et al., 2000). Ocular artifacts were monitored by means of bipolar pairs of electrodes that were positioned at the sub- and supraorbital ridges (vertical electrooculogram, vEOG) and at the external ocular canthi (horizontal electrooculogram, hEOG). The EEG and EOG channels were amplified with a band-pass of 0.01 to 30 Hz and were digitized at 250 Hz.

An offline analysis was performed by means of the BrainVision-Analyzer software (Brain Products, Gilching, Germany). Semiautomated artifact rejection was performed before averaging to discard trials during which an eye movement or any other noncerebral artifact occurred (maximum allowed voltage step per sampling point, $50 \mu\text{V}$; maximum allowed amplitude difference, $200 \mu\text{V}$; minimum allowed amplitude, $-200 \mu\text{V}$; maximum allowed amplitude, $200 \mu\text{V}$; lowest allowed activity [max-min, interval length 100 msec], $0.5 \mu\text{V}$). Ocular correction included semiautomatic blink detection and the application of an established method for ocular artifact removal (Gratton, Coles, & Donchin, 1983). The EEG was then divided into epochs of 1,000-msec duration, starting 100 msec before the onset of stimuli. Error trials (misses, false alarms) were excluded from analysis (misses when the stimulus was a target, false alarms when the stimulus was a distractor). Next, the prestimulus baseline of 100 msec was subtracted from the sampling points. Deflections in the averaged EOG waveforms were small, which indicated good maintenance of fixation. The averaged EEG waveforms were re-referenced to the average of the left and right mastoids. No digital filtering was applied to the data.

Data Analysis

Behavioral task performance was quantified in two ways: First, the median of the response speed at each level of size discriminability was computed for each individual participant, and these median individual response times (RTs) were subjected to statistical analysis. Second, the accuracy of the behavioral responses was computed at each level of size discriminability for each individual participant. The percentage of hits was computed for the target stimuli (S+F+). Percentages of correct rejections were separately computed for each distractor type. Finally, the percentage of correct rejections was computed as an average across all three distractor types. All of these various percentages were transferred into the arcsin transformation prior to statistical analysis.

Mean amplitudes of the N2c evoked by each distractor type were measured in the latency window 230–260 msec with respect to the prestimulus baseline period at electrode Cz, at which the N2c was maximal. Mean amplitudes of the P3a evoked by each distractor type were measured in the latency window 300–500 msec with respect to the prestimulus baseline period at electrode Cz, at which the P3a was maximal.

Mean amplitudes as well as peak amplitudes and latencies of the P3b in response to targets and nontargets were measured in the latency window 275–700 msec with respect to the prestimulus base-

line period at electrode Pz, at which the P3b is usually maximal. Mean amplitudes of the P2a in response to targets and nontargets were measured in the latency window 184–192 msec with respect to the prestimulus baseline period at electrode Fz.

Mean amplitudes of the SN evoked by each distractor type were measured in the latency window 152–252 msec with respect to the prestimulus baseline period at parieto-occipital electrodes (P7, P8, O1, O2; see also Kopp et al., 2007). Furthermore, difference SN waveforms (dSN) were computed by subtracting the standard waveform from the size-overlap waveform (size-dSN) and from the form-overlap waveform (form-dSN), separately for each participant within each of the three perceptual discriminability conditions.

ERPs were averaged separately for all combinations of perceptual discriminability and distractor type. Performance measures and the ERP amplitude measures were subjected to repeated measures ANOVAs using the Greenhouse–Geisser correction. The results of the univariate tests are provided, using a format that gives the uncorrected degrees of freedom and ϵ (Picton et al., 2000). A measure of effect size, η_p^2 , is also provided.

RESULTS

Behavioral Results

Response speed and response accuracy are documented in Table 1. RTs were prolonged when size discriminability was low, as compared with those of the other discriminability conditions. The slowdown was confirmed by a one-way size discriminability ANOVA on RTs [$F(2,46) = 5.2, p < .03, \eta_p^2 = .19, \epsilon = .52$]. Simple contrasts revealed that response speed was slower in the low-discriminability condition than in the other two discriminability conditions [low vs. high condition, $F(1,23) = 5.7, p < .03$; low vs. medium condition, $F(1,23) = 4.9, p < .04$]. Participants performed the required classification at a near-perfect level in the high- and medium-discriminability conditions, as revealed by the hit rates (all means $\geq 99.3\%$) and by the average correct rejection rates (all means $\geq 99.6\%$). The accuracy of performance dropped somewhat in the low-discriminability condition (hit rate = 95.6%; average correct rejection rate = 98.9%). A one-way ANOVA revealed that size discriminability affected hit rates [$F(2,46) = 22.2, p < .001, \eta_p^2 = .49, \epsilon = .84$]. Simple contrasts yielded lower hit rates in the low-discriminability condition than in the other two discriminability conditions [low vs. high condition, $F(1,23) = 32.9, p < .001$; low vs. medium condition, $F(1,23) = 21.2, p < .001$]. Another one-way ANOVA revealed that size discriminability affected

average correct rejection rates [$F(2,46) = 14.3, p < .001, \eta_p^2 = .38, \epsilon = .54$]. Simple contrasts yielded lower correct rejection rates in the low-discriminability condition than in the other two discriminability conditions [low vs. high condition, $F(1,23) = 16.6, p < .001$; low vs. medium condition, $F(1,23) = 12.9, p < .002$].

When the correct rejection rates of the various types of distractors were tested in a two-way stimulus category (size distractor, form distractor, standard distractor) $\times$ size discriminability ANOVA, both main effects [stimulus category, $F(2,46) = 14.3, p < .001, \eta_p^2 = .38, \epsilon = .73$; discriminability, $F(2,46) = 13.7, p < .001, \eta_p^2 = .37, \epsilon = .98$], as well as the interaction between stimulus category and discriminability [$F(4,92) = 24.9, p < .001, \eta_p^2 = .52, \epsilon = .67$], proved significant. Separate ANOVAs on correct rejection rates were performed in each size discriminability condition to further parse the two-way interaction. The correct rejection rates related to the various distractors differed in the high-size-discriminability condition [$F(2,46) = 6.6, p < .02, \eta_p^2 = .22, \epsilon = .63$]. Simple contrasts revealed that the correct rejection rates related to the form distractor [$F(1,23) = 4.6, p < .05, \eta_p^2 = .17$] as well as to the size distractor [$F(1,23) = 11.4, p < .004, \eta_p^2 = .33$] were lower than the correct rejection rate related to the standard distractor. The correct rejection rates related to the various distractors differed also in the medium-size-discriminability condition [$F(2,46) = 5.1, p < .02, \eta_p^2 = .18, \epsilon = .79$]. Simple contrasts revealed that the correct rejection rates related to the size distractor [$F(1,23) = 6.0, p < .03, \eta_p^2 = .21$], but not those related to the form distractor [$F(1,23) < 1$], were lower than the correct rejection rate related to the standard distractor. The correct rejection rates related to the various distractors differed also in the low-size-discriminability condition [$F(2,46) = 45.6, p < .001, \eta_p^2 = .67, \epsilon = .87$]. Simple contrasts revealed that the correct rejection rates related to the form distractor [$F(1,23) = 72.2, p < .001, \eta_p^2 = .76$] as well as to the size distractor [$F(1,23) = 6.5, p < .02, \eta_p^2 = .22$] were lower than the correct rejection rate related to the standard distractor.

ERP Results: General N2c and P3a Data

Figure 2 plots grand-average ERPs at midline electrodes that were obtained in response to the nontarget stimuli, separately for high (Figure 2, upper panel), medium (Figure 2, center panel), and low (Figure 2, lower panel) size discriminability, with the three types of distractors overlaid (form distractor, size distractor, standard distractor).² A two-way distractor type $\times$ size discriminability ANOVA was performed on the N2c mean amplitudes at Cz (Figure 2, center panel). Distractor type [$F(2,46) = 6.0, p < .006, \eta_p^2 = .21, \epsilon = 1.0$], discriminability [$F(2,46) = 6.0, p < .02, \eta_p^2 = .21, \epsilon = .67$], and the interaction of distractor type $\times$ discriminability [$F(4,92) = 7.5, p < .001, \eta_p^2 = .25, \epsilon = .72$] proved significant. Another two-way distractor type $\times$ size discriminability ANOVA was performed on the P3a mean amplitudes at Cz (Figure 2, center panel). Discriminability [$F(2,46) = 12.3, p < .001, \eta_p^2 = .35, \epsilon = .96$] and the interaction of distractor type $\times$ discriminability [$F(4,92) = 5.2, p < .005, \eta_p^2 = .19, \epsilon = .68$] were significant.

Table 1
Response Speed and Response Accuracy
As a Function of Size Discriminability

	High		Medium		Low	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
RT	403	56	406	57	447	94
Hits (S+F+)	99.5	1.1	99.3	1.0	95.6	5.3
CR (S+F-)	99.2	1.5	99.2	1.2	99.5	0.9
CR (S-F+)	99.8	0.4	99.9	0.4	97.4	2.9
CR (S-F-)	100	0	99.8	0.5	99.9	0.2
CR (avg)	99.7	0.5	99.6	0.6	98.9	1.2

Note—RT, response time (in milliseconds); Hits (as a percentage); CR, correct rejections (as a percentage); S+F+, target stimulus; S+F-, size distractor; S-F+, form distractor; S-F-, standard distractor; avg, average across all distractor types.

Figure 2. The grand-average ERP waveforms at midline electrodes (Fz, Cz, Pz) separately for high (upper panels), medium (center panels), and low (lower panels) size discriminability. The waveforms obtained from form distractors (medium gray; online version red), size distractors (dark gray; online version blue), and standard distractors (light gray; online version green) are overlaid.

Tests of the N2c/P3a Enhancement Prediction

In order to directly test the enhancement prediction, separate ANOVAs on the N2c and the P3a mean amplitudes were performed in each size discriminability condition to further parse the two-way interaction. The N2c that was evoked by the various distractors differed in the high-size-discriminability condition [$F(2,46) = 11.8, p < .001, \eta_p^2 = .34, \varepsilon = .81$]. Simple contrasts revealed that the N2c in response to the form distractor did not differ from the N2c evoked by the standard distractor [$F(1,23) < 1$]. In contrast, the N2c in response to the size distractor differed significantly from the N2c evoked by the standard distractor [$F(1,23) = 25.3, p < .001, \eta_p^2 = .40$]. The N2c that was evoked by the various distractors differed in the medium-size-discriminability condition [$F(2,46) = 4.8, p < .02, \eta_p^2 = .17, \varepsilon = .95$]. Simple contrasts revealed that the N2c in response to the form distractor did not differ from the N2c evoked by the standard distractor [$F(1,23) < 1$]. In contrast, the N2c in response to the size distractor differed significantly from the N2c evoked by the standard distractor [$F(1,23) = 8.2, p < .01, \eta_p^2 = .26$]. The N2c differences in the low-size-discriminability condition failed to reach an acceptable level of statistical significance [$F(2,46) = 1.7, p = .21, \eta_p^2 = .07, \varepsilon = .72$].

The P3a that was evoked by the various distractors differed in the high-size-discriminability condition [$F(2,46) = 5.8, p < .02, \eta_p^2 = .20, \varepsilon = .66$]. Simple contrasts revealed that the P3a in response to the form distractor differed from the P3a evoked by the standard

distractor [$F(1,23) = 6.7, p < .02, \eta_p^2 = .22$], and that the P3a in response to the size distractor differed significantly from the P3a evoked by the standard distractor [$F(1,23) = 8.7, p < .01, \eta_p^2 = .27$]. The P3a's evoked by the various distractors did not differ from each other in the medium-size-discriminability condition [$F(2,46) < 1$]. The P3a that was evoked by the various distractors differed in the low-size-discriminability condition [$F(2,46) = 4.1, p < .04, \eta_p^2 = .15, \varepsilon = .75$]. Simple contrasts revealed that the P3a in response to the form distractor differed from the P3a evoked by the standard distractor [$F(1,23) = 6.5, p < .02, \eta_p^2 = .22$], whereas the P3a in response to the size distractor did not differ significantly from the P3a evoked by the standard distractor [$F(1,23) < 1$].

Tests of the N2c/P3a Crossover Prediction

In order to directly test our crossover prediction, a two-way distractor type $\times$ size discriminability ANOVA was performed on the N2c mean amplitudes in response to the size and form distractors that were obtained in the high- and low-size-discriminability conditions, respectively. Solely the interaction of distractor type $\times$ discriminability [$F(1,23) = 14.4, p < .002, \eta_p^2 = .39$] proved significant, thereby confirming the presence of an N2c amplitude crossover effect. Likewise, the interaction of distractor type $\times$ discriminability [$F(1,23) = 7.3, p < .02, \eta_p^2 = .24$] proved significant when another two-way distractor type $\times$ size discriminability ANOVA was performed on the P3a mean amplitudes, thereby confirming the presence of a P3a amplitude crossover effect.

Figure 3. The grand-average ERP waveforms at midline electrodes (Fz, Cz, Pz) separately for high (dark gray; online version blue), medium (light gray; online version green), and low (medium gray; online version red) size discriminability, with waveforms obtained from targets (solid) and nontargets (dashed) overlaid. Scaling (abscissa, ordinate axes) is optimized for visibility of the parietal P3b in the left panels. Scaling (abscissa, ordinate axes) is optimized for visibility of the frontal P2a in the right panels.

Additional ERP Results: P3b, P2a, and SN

Figure 3 plots grand-average ERPs at midline electrodes that were obtained in response to target stimuli that were compared with ERPs obtained in response to the average of all nontarget stimuli. The target stimuli (+7.3 μV mean amplitude at Pz in the latency range of 275–700 msec), but not the nontarget stimuli (+2.6 μV mean amplitude at Pz in the same latency range), evoked a large P3b with parietal maximum (Figure 3, left panel). The presence of a target-P3b at Pz was confirmed by a two-way stimulus category (target, nontarget) $\times$ size discriminability ANOVA that yielded a highly reliable stimulus category effect [$F(1,23) = 82.3, p < .001, \eta_p^2 = .78$].

P3b peak amplitudes and latencies were subjected to two separate one-way size discriminability ANOVAs in order to evaluate the influence of the manipulation of size discriminability on the P3b. The P3b peak amplitudes differed between discriminability conditions [$F(2,46) = 8.0, p < .003, \eta_p^2 = .26, \varepsilon = .91$]. Simple contrasts revealed that the P3b peak amplitude was reduced in the low-size-discriminability condition as compared with the other two discriminability conditions [high vs. low, $F(1,23) = 14.9, p < .02, \eta_p^2 = .39$; medium vs. low, $F(1,23) = 4.3, p = .05, \eta_p^2 = .16$]. The P3b peak latencies also differed between discriminability conditions [$F(2,46) = 9.8, p < .001, \eta_p^2 =$

.30, $\varepsilon = .94$]. Simple contrasts revealed that the P3b peak latency was prolonged in the low-size-discriminability condition as compared with the other two discriminability conditions [high vs. low, $F(1,23) = 14.6, p < .02, \eta_p^2 = .39$; medium vs. low, $F(1,23) = 11.4, p < .004, \eta_p^2 = .33$].

The target stimuli evoked an enhanced P2a with frontal maximum (+2.0 μV mean amplitude at Fz in the latency range 184–192 msec) as compared with the nontarget stimuli (+0.5 μV mean amplitude at Fz in the latency range 184–192 msec; Figure 3, right panel). The presence of an enhanced target P2a at Fz was confirmed by a two-way stimulus category (target, nontarget) $\times$ size discriminability ANOVA, yielding a reliable stimulus category effect [$F(1,23) = 43.3, p < .001, \eta_p^2 = .65$], without notable effects of discriminability or of the interaction between stimulus category and discriminability.

Figure 4 plots grand-average ERPs in response to size, form, and standard distractors at occipitoparietal electrodes, separately for high, medium, and low size discriminability. Figure 5 plots grand-average difference waves at occipitoparietal electrodes, separately for high (Figure 5, upper panel), medium (Figure 5, center panel), and low (Figure 5, lower panel) size discriminability. The form-SN waves were computed by subtracting the standard distractor ERP from the form distractor ERP. The size-SN waves

Figure 4. The grand-average ERP waveforms at occipitoparietal electrodes (P7, P8, O1, O2) for high (upper panels), medium (central panels), and low (lower panels) size discriminability. The waveforms obtained from size and standard distractors are overlaid in the upper graphs; the waveforms obtained from form and standard distractors are overlaid in the lower graphs.

were computed by subtracting the standard distractor ERP from the size distractor ERP. A four-way stimulus category (form, size) $\times$ size discriminability $\times$ hemisphere (left, right) $\times$ position (O, P) ANOVA was performed on SN mean amplitudes in the latency range 152–252 msec. Solely the two-way interaction of stimulus category $\times$ discriminability [$F(2,46) = 6.9, p < .005, \eta_p^2 = .23, \varepsilon = .85$] proved significant; no other main or interaction effect attained statistical significance. Separate ANOVAs on mean SN amplitudes were performed in each size discriminability condition to further parse the two-way interaction. Form-SN and size-SN amplitudes did not differ in the high- [$F(1,23) < 1$] or in the medium- [$F(1,23) < 1$] discriminability condition. The amplitude difference between the form-SN and the size-SN proved significant in the low-size-discriminability condition [$F(1,23) = 18.0, p < .001, \eta_p^2 = .44$]. The difference between the form-SN and the size-SN was modulated by region [$F(1,23) = 8.6, p < .01, \eta_p^2 = .27$; occipital $>$ parietal] and by hemisphere [$F(1,23) = 7.6, p < .02, \eta_p^2 = .25$; left $>$ right].

DISCUSSION

The N2c and P3a results are, by and large, in accordance with the enhancement prediction that nontargets

that share one feature with the target elicit response conflict or a need to inhibit a prepared response, and thus larger N2c and P3a amplitudes, as compared with nontargets that share no feature with the target. Specifically, we found enhanced N2c and P3a amplitudes in response to the size distractor in the high-size-discriminability condition, indicating that the presence of a target-compatible size feature apparently induced response conflict or the need to inhibit a prepared response (cf. the introduction). Under low size discriminability, the temporal advantage of size processing over form processing seems to have disappeared, and the P3a, but not the N2c, data suggest that form could be processed faster than size under these circumstances.

The response accuracy results provide some additional information about the processing of the two stimulus dimensions (size, form). Response accuracy was generally excellent, but it dropped somewhat in the low-size-discriminability condition. False alarm rates in this discriminability condition are particularly instructive (Table 1): We observed around 2.5% false alarms in response to form distractors, 0.5% false alarms in response to size distractors, and no more than 0.1% false alarms in response to standard distractors. Erroneous responses to form distractors occur when the target-compatible form

Figure 5. The grand-average selection negativity (SN) difference waveforms at occipitoparietal electrodes (P7, P8, O1, O2) for high (upper panels), medium (central panels), and low (lower panels) size discriminability. The black lines show form-SN waves, computed by subtracting the standard distractor ERP from the form distractor ERP (cf. Figure 4, lower graphs). The gray lines show the size-SN waves, computed by subtracting the standard distractor ERP from the size distractor ERP (cf. Figure 4, upper graphs).

features are identified correctly, but target-incompatible size features are incorrectly identified as being target compatible. Erroneous responses to size distractors occur when the target-compatible size features are identified correctly, but target-incompatible form features are identified incorrectly as being target compatible. The fivefold higher false alarm rate in response to form distractors as compared with size distractors suggests that size discriminations were less accurate than form discriminations in the low-size-discriminability condition.

Overall, these ERP data ought to be regarded as converging evidence against fully discrete models of information transmission between stimulus recognition and response preparation (Miller & Hackley, 1992; Osman et al., 1992). We derived the enhancement prediction from the ADC model (Miller, 1982, 1983), according to which response preparation can begin only after recognition processes have activated a code (Posner, 1978) used in categorizing a stimulus. It is natural to assume that these internal codes are equivalent to dimension-specific (size, form) target-compatibility categorizations (i.e., the $S \pm$ and $F \pm$ categorizations) in the present experiment.

We manipulated size discriminability, and we claim that this manipulation affects the decision time for size discriminations. Furthermore, we do claim that the N2c and P3a are cortical correlates of response conflict or the need to inhibit a prepared response. We infer from the observed N2c/P3a amplitude crossover that form discriminations take longer than size discriminations when size discriminations are easy, whereas size discriminations take longer than form discriminations when size discriminations are difficult. Thus, we offer the experimental design as a diagnostic tool for the assessment of the (otherwise unobservable) relative speed of perceptual processing

of two (or more) visual dimensions. Overall, this experimental design can serve as a combined psychophysical–psychophysiological approach to the dynamics of the availability of partial information from different types of perceptual processing. Specifically, by manipulating the perceptual discriminability of visual features systematically, feature-specific quantitative models of partial transmission of information from particular visual modules to response preparation seem conceivable.

The N2c and P3a findings cannot be discounted by either ERP component overlap or the effects of task-difficulty differences across the levels of size discriminability, as indicated by response latency and response accuracy. First, with regard to the component overlap issue (Luck, 2005), it must be kept in mind that the labels N2c and P3a designate solely negative and positive voltage peaks in the observed ERP waveform that occur in temporal proximity. However, the observation of an increase in amplitude of the N2c and of the P3a cannot be explained by assuming either an increased negative deflection in the N2c–P3a latency range alone, or an increased positive deflection in the N2c–P3a latency range alone; both types of modulations (one negative, one positive) of the ERP waveforms evidently co-occurred. Second, the crossover of N2c and P3a amplitudes cannot be attributed to the difficulty of the visual discrimination process (Philiastides, Ratcliff, & Sajda, 2006). This holds because the N2c and P3a amplitudes were observed under high and low size discriminability, respectively.

It should be noted, however, that N2c and P3a amplitude enhancement presupposes that the processing of the target-compatible feature terminated earlier than the processing of the target-incompatible feature. An opportunity for response preparation based on preliminary information

is given only under these circumstances, and no response preparation is expected to occur if the processing of the target-compatible feature terminates at the same time or even later than the processing of the target-incompatible feature. The observed pattern of ERP results leads to the conclusion that the N2c and P3a amplitude enhancement occurred contingent on preliminary response preparation rather than on a global need to modify a decision. Whether the N2c is related to a need to inhibit a prepared response or to a global decision conflict is still a controversial issue in the literature (Folstein & Van Petten, 2008; Kopp, Mattler, et al., 1996; Kopp, Rist, & Mattler, 1996; Yeung et al., 2004). Folstein and Van Petten concluded in their extensive review of research on the N2 component of the ERP that there may exist dissociable N2 components with an anterior scalp distribution, one of which is clearly related to cognitive control. The bulk of the available evidence about the functional significance of the N2c suggests that this ERP component is related to the need to inhibit a prepared response (Kopp, Mattler, et al., 1996; Kopp, Rist, & Mattler, 1996). We do not claim that the N2c and the P3a are similarly related to cognitive control. The bulk of the available P3a studies points in the direction that the P3a is functionally related to attention switching (Friedman et al., 2001; Kopp, Tabeing, Moschner, & Wessel, 2006; Squires et al., 1975). Given this, it is possible that the P3a reflects a dimensional attention switch between preliminary and secondary stimulus information.

In a recent ERP study, Folstein, Van Petten, and Rose (2008) also used stimuli consisting of pairs of visual features, with response governed by the conjunction of particular features. Folstein et al. did not find larger anterior N2s in response to stimuli with two features that suggest different responses, as compared with stimuli whose two features were associated with the same response. This N2 result, which stands in direct contrast with that of the present data, seems to challenge the generality of the present results and/or the specific circumstances under which partial transmission from stimulus recognition to response preparation can take place (see also Miller, 1983). In our own precursor ERP study (Kopp et al., 2007), participants did classify two-dimensional visual stimuli with dimensions color (red, blue) and form (rectangle, ellipse). We then used the same logic as in the present study to ask which of these two dimensions was resolved faster. The N2c and P3a amplitude results suggested that form was processed more slowly than color, even if color discriminability was very difficult.

The experimental designs of two psycholinguistic ERP studies (Rodríguez-Fornells, Schmitt, Kutas, & Münte, 2002; Schmitt, Schiltz, Zaake, Kutas, & Münte, 2001) also closely paralleled the present experiment. Schmitt et al. used the same logic as in the present study, and then used the latency of the peak of the N2 to ask which of two dimensions (semantic, syntactic) was resolved first. In the other study (Rodríguez-Fornells et al., 2002), semantic and phonologic dimensions were examined. The latencies of the N2 peaks reversed, depending on the modality of the stimulation (visual, auditory)—a manipulation that apparently reversed which dimension was accessed more quickly.

Additional ERP results pertain to the posterior SN. As revealed by the SN, selective visual attention to target-compatible features was observable in both feature dimensions in high- and medium-size-discriminability conditions. In the low-size-discriminability condition, selective allocation of attention to the target-compatible size feature decreased, whereas selective attention to the target-compatible form feature remained stable. The SN findings indicate that selective visual attention was allocated to target-compatible features (Anllo-Vento, Schoenfeld, & Hillyard, 2004; Smid, Jakob, & Heinze, 1997, 1999). Selective attention is usually considered to enhance neural responses (“attentional gain”) in a range of cortical areas (Luck, Woodman, & Vogel, 2000).

An important characteristic of our present experiment was that stimuli were counterbalanced across participants (cf. the Method section, Figure 1). The pursuit of this experimental procedure guarantees that ERP waveforms elicited by different types of distractors are, within one particular level of size discriminability, elicited by identical physical stimuli. This principle has been very important for attention-related ERP research (Anllo-Vento et al., 2004; Luck, 2005). This is because attentional modulations of ERP waveforms can be interpreted as reflecting voluntary, rather than reflexive, aspects of attention (Corbetta & Shulman, 2002; Pashler, Johnston, & Ruthruff, 2001) only when physical differences between stimuli can be excluded as the source of ERP waveform modulations. Several authors have argued that visual selective attention is predominantly reflexive (Itti & Koch, 2001; Theeuwes, 1992). This view proposes that salient visual events attract attention irrespective of the goals of the observer. However, observers often adopt a deliberate voluntary attentional set for target-compatible features when searching for particular visual target stimuli (Serences et al., 2005). The SN findings suggest that reflexive and voluntary aspects of selective visual attention do actually interact. In particular, voluntary attention seems to be allocated dynamically, in accord with the salience of target-defining features. Target-compatible size features capture attention mainly when size is a very salient stimulus feature. When size discriminability is diminished, attentional amplification of the target-compatible form feature obviously gains importance over amplification of the size feature. The SN data suggest adaptive changes in attentional prioritization of size and form features when the salience of the size dimension diminished.

We will also briefly comment on another ERP finding. Target detection led to the emergence of the classical parietal P3b, but target stimuli also evoked a frontal P2a. The classical parietal P3b (Polich, 2007) peaked at a latency of around 400 msec (375 msec high-, 386 msec medium-, and 416 msec low-size-discriminability conditions). However, the P3b was not the first sign that the stimulus has been categorized as a target, according to the conjunctive rules of our task. The P2a peaked long before the P3b showed its peak. Thus, the evaluation of stimuli as matching a designated target took place much faster than would be suspected on the basis of the latency of the P3b (McCarthy & Donchin, 1981).

The major goal of the present work was to develop a new experimental method for analyzing details of cognitive processes that are related to partial information transmission from stimulus recognition to response preparation. We offer a simple experimental tool in combination with the assessment of ERPs in the no-go trials of the task (Luck, 2005). The design offers a method to infer the relative processing times of two perceptual dimensions and also an approach to infer details of partial transmission of information from stimulus recognition to response preparation. In the present study, we focused on the assessment of the N2c and P3a components of the ERP in the no-go trials, but we also measured the SN, P3b, and P2a. Earlier scientific studies that explored the nature of this transmission of information were mainly based on the LRP (Miller & Hackley, 1992; Osman et al., 1992). Future studies should pursue an integrative approach in which the N2c, P3a, SN, P3b, P2a, and the LRP are considered simultaneously. Our experimental design can be easily accommodated to measure the LRP in addition to the ERPs in the no-go trials of the task.

AUTHOR NOTE

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NOTES

1. Participants were identical to those who took part in our earlier study (Kopp et al., 2007). In fact, both experiments were conducted in one session.

2. Careful readers will recognize an amplitude enhancement of P1 at Pz in response to the size distractor (see also Busch, Debener, Kranczoch, Engel, & Herrmann, 2004, for size-related ERP findings) when size discriminability was high. In a similar vein, an augmented P2a amplitude at Fz was elicited by the form distractor under low size discriminability. We also note a phasic positivity at Pz in response to the size distractor under high size discriminability and a more sustained positivity at Pz in response to the form distractor under low size discriminability. The phasic parietal positivity may represent the volume-conducted P3a, or it may constitute independent neural activity. The sustained parietal positivity may represent the latency-jittered P3a, or it may constitute independent neural activity. We do not comment further on these apparent modulations of ERP waveforms because their appearance is in none of these cases essential for our argument.

(Manuscript received December 1, 2008;
revision accepted for publication November 25, 2009.)