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Accelerated and amplified neural responses in visual discrimination: Two features are processed faster than one

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Psychological and neurophysiological models of visual processing have traditionally emphasized hierarchical models to explain how separate features of visual stimuli are combined. This concept has been challenged recently with the demonstration of simultaneous activation of multiple visual areas and rapid feedback to primary cortices. Here, we show human visual processing may involve similar mechanisms. Subjects discriminated targets from nontargets as a function of shape, color, or the conjunction of these features while event-related brain potentials (ERPs) were recorded. ERP components from 100 to 200 ms across posterior occipital–temporal cortices were fastest and largest for conjunction targets. These enhanced early responses were followed by task-specific sustained posterior activity (300–500 ms). Faster reaction times were correlated with enhanced and faster early processing in the visual ventral areas. These data demonstrate the human visual system conjoins features rapidly, accelerating and amplifying the processing of relevant stimulus dimensions.

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There is considerable discussion in the cognitive neurosciences literature on how and when the separate perceptual features of objects are combined (the 'binding problem', [Neuron, 1999](#)). Visual search paradigms, where participants search for a target embedded in an array of distractors, are frequently used to investigate this problem. Processing time (e.g., reaction times (RTs)) is typically affected by manipulations such as array size when a conjunction of features defines the target, but not when a

single feature defines the target. These data have been frequently explained using hierarchical models (e.g., [Riesenhuber and Poggio, 1999](#); [Treisman, 1988](#)), which argue that separate features are processed first and in parallel, and subsequently the features are conjoined, such that items can be identified, producing an item-by-item search. However, in the classical stimulus array tasks, the time taken to bind features is confounded with the time spent searching the array, thus contaminating the estimated timing for feature binding. When single stimuli are presented serially, and subjects judge if single features or feature conjunctions are present, fast RTs for conjunction stimuli can be seen ([Woods et al., 1998](#)). This effect was particularly strong when one of the features to be conjoined was color. Visual stimuli requiring the conjunction of three visual features have also been reported to elicit faster RTs ([Wolfe et al., 1989](#)). However, according to hierarchical, sequential models of sensory processing, neither RTs nor the neural response to conjunction targets should be faster than to single feature targets.

Alternative models also allow for separate processing streams, but argue that feature integration can occur rapidly via recurrent and/or lateral interactions (e.g., [Bartels and Zeki, 1998](#); [Lamme and Roelfsema, 2000](#)). Psychophysical data suggest the features color and form can be integrated within 60 ms following stimulus onset ([Moutoussis and Zeki, 1997](#); [Viviani and Aymoz, 2001](#)). Both human and animal studies show that numerous visual areas are activated almost simultaneously following visual input ([Vanni et al., 2001](#)) and primary sensory cortices receive very rapid feedback ([Bullier, 2001](#); [Foxy and Simpson, 2002](#)). Thus, the distributed nature of connections in the visual system suggests the possibility for rapid binding and task-specific modulation of early responses in visual cortices; here we present evidence of this in real-time measures of human brain function.

Event-related potentials (ERPs) were recorded while subjects discriminated visual targets from nontargets. Across four blocks of trials in a sustained-attention paradigm, single stimuli that varied in shape and/or color were presented sequentially. In each block, one specific color/shape combination was the target. Depending on the

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features of the nontarget stimuli, targets were identified based on one of the two features of the target (single-feature shape; single-feature color), both features (conjunction), or either feature (redundant). The full temporal and spatial extent of the neurophysiological data was analyzed to determine the differences between single and conjunction target processing, and whether they related to behavior. These data illustrate that the neural response to conjunctions of color and shape shows acceleration and amplification of short-latency ERP components and that this facilitation impacts on behavior.

Materials and methods

Twenty-nine adults (11 men) were tested (21–47 years, mean = 30.9 ± 6.2 years). All gave informed consent and the institute's ethics committee approved the procedure.

Procedure

This protocol was modified from Stuss et al. (1989) to examine conjunction processing in children (Taylor et al., 2003). Due to the time constraints associated with testing children, four blocks of 96 stimuli were run, with targets presented randomly on 25% of trials. Each block was preceded by eight practice trials. Subjects pressed a keyboard key with their dominant hand to targets and another key with their non-dominant hand to nontargets. They were instructed to respond as quickly as possible, without making errors. For all tasks, instructions referred to both the color and shape of the target stimulus, and no instructions to attend to any specific features were given. Stimuli were presented one at a time, centrally, on a computer screen for 650 ms with a variable inter-stimulus interval of 1–2 s. Stimuli subtended approximately 4° visual angle and were circles, triangles, diamonds, or crosses (Fig. 1). They were displayed using MEL2.0 software. The four colors used were in upper VGA color space: blue (21/21/63), yellow (63/63/21), red (63/21/21), and magenta (63/21/63). Four blocks were run in a fixed sequence: single-feature shape, single-feature color, feature conjunction, and redundant. This sequence was deliberate in order to measure the change in processing from single feature to feature conjunction and back to single-

feature targets. Two different target sets were used to ensure that the effects were not due to specific target features. As there were no differences in the ERPs between the two target sets, the data were combined for analysis.

Single-feature shape

Single-colored (e.g., blue) stimuli of various shapes were presented; the target was a specified shape and color (e.g., blue circle), thus subjects had to discriminate targets on the basis of shape.

Single-feature color

Single-shaped stimuli (e.g., circles) of various colors were presented; the target was a specified color and shape (e.g., magenta circle), thus subjects discriminated on the basis of color.

Feature conjunction

Variouly colored and shaped stimuli were presented; the target was a conjunction of color and form (e.g., yellow cross). The nontargets could be the same color as the target (e.g., yellow but not crosses—discriminate on shape, 25%), or the same shape (e.g., crosses of different colors—discriminate on color, 25%), or neither the same color nor the same shape (discriminate on either feature, 25%). Subjects had to discriminate targets on the basis of both color and shape.

Redundant

This task was as visually complex as the feature-conjunction block in that the stimuli were of various colors and shapes. However, only a single feature was required to discriminate targets (e.g., red triangle) from nontargets. In this block, the nontargets shared no feature with the target (neither red nor triangles), thus subjects only needed to use color or shape for successful discrimination. The redundant task differed from the single-feature shape and color tasks, which can be considered “true” single-feature tasks, in that subjects' strategies were not determined by the imposed stimulus manipulations. Thus while subjects only needed one feature to successfully identify the target, there is the possibility that subjects could maintain a conjunction strategy in this block (i.e., not switching set, Stuss et al., 1994).

ERP recording and measurement

The ERPs were recorded from 30 electrodes applied with an ECI electrode cap in the 10–10 system, which included four posterior–inferior electrodes (P9, P10, CB1 and CB2). EOG electrodes were placed at the outer canthus and supraorbital ridge of the left eye. ERPs were collected on a NeuroScan system at 500 Hz and a band-pass of 0.1–30 Hz, with SynAmps amplifiers. The recording interval was 1.5 s, with a 100-ms pre-stimulus baseline. Cz was the reference lead during the recording. The use of the common average reference is the recommended reference according to the international ERP guidelines (Picton et al., 2000), regardless of the modality of stimuli, providing that one has even and full head coverage. As our electrode caps included electrodes inferior to the “horizon” and were evenly distributed over the head, the average common reference was most suitable for these data and was used for these analyses.

Off-line averaging was conducted, and any trials with EOG or movement artifact ($\pm 90 \mu\text{V}$) from 0 to 500 ms were rejected. The trials were averaged within block according to the target/nontarget

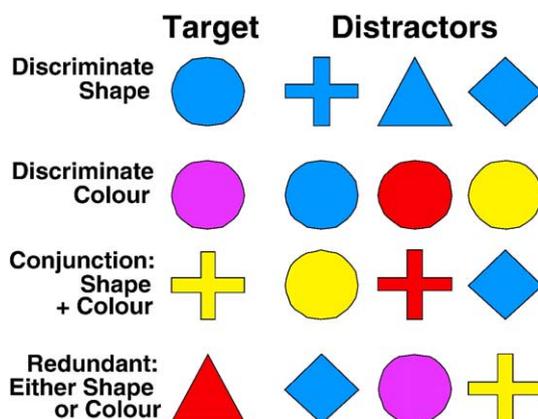


Fig. 1. Stimuli. Examples of stimuli used as targets and distractors in single feature (shape, color), feature conjunction, and redundant tasks.

categories; trials with incorrect behavioral responses were rejected. Early visual processing was assessed by measuring the P1 and N1 components (peak latency from stimulus onset and amplitudes at the peaks' maxima) at eight posterior–temporal–occipital sites (P7/P8, P9/P10, CB1/CB2, O1/O2). The epoch analyzed was from 0 to 500 ms, a time window in which target discrimination would occur. For the four target conditions presented here, 88% of target trials were accepted for averaging (21.1 ± 1.8). The two EOG channels were not included in the analyses.

Data analyses

Two aspects of the full ERP dataset were examined. First, the impact of the type of discrimination (“true” single feature vs. conjunction vs. redundant single feature) on target ERP waveforms was identified. Second, to see if the observed ERP differences were related to behavior, the correlations of ERP amplitudes with RT were examined. To do this, the multivariate partial least squares (PLS) analysis (McIntosh et al., 1996, 1998, 1999) was used. PLS has been extended recently to spatiotemporal data (see McIntosh and Lobaugh, 2004 for review). This approach allows the determination of all time points and electrodes that contribute to differences in the ERP waveforms or correlate with behavior. Thus, for example, if multiple time points and/or multiple channels reflect a particular distinction among waveforms, these time points and channels will be identified as belonging to the same effect.

As mentioned above, the TaskPLS was conducted to identify differences among the ERP waveforms related to target type¹. Two methods have been used for TaskPLS: analysis of the covariance between the data and a set of $n_{\text{tasks}} - 1$ orthogonal contrasts (e.g., Lobaugh et al., 2001; McIntosh et al., 1996), and a mean-centered approach (e.g., Itier et al., 2004). These two techniques lead to identical conclusions (McIntosh and Lobaugh, 2004). The mean-centering approach was used here. First, a data matrix is created containing subjects and conditions in the rows, and the ERP amplitudes for all time points and all channels in the columns. Means are created for each task for each column in the ERP amplitude data matrix. These task means are then subtracted from the grand mean to produce a mean-centered deviation matrix ($n_{\text{tasks}} \times [n_{\text{time points}} * n_{\text{channels}}]$). Singular value decomposition (SVD) is applied to the deviation matrix. The second analysis was a BehaviorPLS, which examined the correlations of RT with ERP amplitudes. Within-task correlations of RT and ERP amplitudes are generated and stacked into a single matrix ($n_{\text{tasks}} \times [n_{\text{time points}} * n_{\text{channels}}]$) and SVD is applied to this RT–ERP correlation matrix.

The latent variables derived from the SVD each contain three outputs that are used to interpret the relationships between ERP amplitudes and task design or behavior. The first is a vector of singular values, which represents the covariance of the experimental effect with the ERP amplitude. The second and third outputs contain the structure of the latent variables and are orthogonal pairs of vectors (saliences). One vector in each pair defines the contrasts among conditions (design saliences, TaskPLS), or the strength of the within-task RT–ERP correlations

(behavior saliences, BehaviorPLS). The other vector (electrode saliences) identifies where, in time and space, the effects for each latent variable are expressed. The magnitude and sign of the electrode saliences indicate the strength and direction of the identified differences among the conditions at each time point. In the TaskPLS, the number of latent variables available for inspection is equal to $n_{\text{tasks}} - 1$, or the number of degrees of freedom in the design. For the BehaviorPLS, the number of latent variables equals the number of task conditions.

To avoid arbitrary decisions on the number of latent variables to consider, the LVs are assessed statistically. This evaluation is achieved by using permutation tests (500 samples) to assess the strength of the observed patterns (Lobaugh et al., 2001). For each subject, sampling without replacement is used to reassign the order of the task conditions and PLS is recalculated for each sample. The number of times a permuted singular value exceeds the observed singular value provides an exact probability for each latent variable, assessing whether the latent variable is sufficiently strong to be distinguished from noise. Bootstrap resampling (200 samples) was used to assess the stability of the electrode saliences. Here, subjects are sampled with replacement (keeping task conditions fixed) and PLS is recalculated. The standard errors (Lobaugh et al., 2001) of the electrode saliences are estimated from the sampling

Table 1
Mean reaction times, peak latencies, and amplitudes for targets and nontargets for the shape, color, conjunction, and redundant tasks

Stimulus	Reaction time (ms) ^a	P1 ^b		N1 ^c	
		Latency (ms)	Amplitude (μV)	Latency (ms)	Amplitude (μV)
Targets					
Shape	433.6 [^]	120.0 [»]	2.04	171.6 [□]	−4.15 [□]
Color	449.3	116.5	2.19	175.7	−5.04 [□]
Conjunction	456.0	114.5 [«]	1.79	160.0 ^{§†}	−8.03 ^{§††}
Redundant	451.6	115.0 [«]	1.62	167.9	−5.70
Nontargets					
Shape	415.5	117.0	1.37	162.9 [□]	−6.33 [□]
Color	419.9	119.7 [»]	1.91	173.1	−3.81 [□]
Conjunction: Color ^d	441.4 ^{^^}	115.6	1.77	162.5	−8.08
Conjunction: Shape	437.8 ^{^^}	116.9	2.11	167.1 [§]	−5.07 [§]
Conjunction: Either	417.7	118.3 [»]	2.43	172.1 [§]	−4.90 [§]
Redundant	409.0	119.0	1.59	167.5	−5.78

^a Reaction time: Target RTs were fastest to shape targets ([^]). Nontarget RTs were slowest to Conjunction nontargets discriminated on the basis of shape and colour (^{^^}).

^b P1 component: Conjunction and redundant targets ([«]) had shorter P1 latencies than single-feature shape targets, single-feature colour nontargets, and conjunction nontargets discriminated by either feature ([»], Task × Target/Nontarget, $F(2.67, 74.84) = 3.34$, $P < 0.03$).

^c N1 component: Task × Target/Nontarget interactions were found for N1 latency ($F(2.07, 58.05) = 4.09$, $P < 0.02$) and amplitude ($F(2.56, 80.02) = 27.21$, $P < 0.001$). Target/Nontarget differences were seen only for the single-feature ([□]) and conjunction tasks ([§]). Conjunction target latencies were faster than all other conditions except for nontargets in the discriminate shape task ([†]). Conjunction target amplitudes were larger than all other conditions (^{††}).

^d For the conjunction task, the three types of nontargets were discriminated on the basis of shape, color, or either feature.

¹ A separate analysis of the 6 nontarget conditions was also conducted, but the results did not indicate any clear patterns with respect to stimulus features (color or shape) or task (single, conjunction, redundant). As the focus of the work was on target discrimination, the nontarget PLS results are not presented.

distribution of the bootstrapped saliences. The ratio of a salience to its standard error is approximately equivalent to a z score. For these data, bootstrap ratios $>|3.0|$ are shown for the TaskPLS and bootstrap ratios $>|2.5|$ for the BehaviorPLS.

Bootstrap resampling was also used to calculate the 95% confidence interval around the obtained RT–ERP correlations in the BehaviorPLS analysis. The correlation was considered reliable if the confidence interval did not include zero.

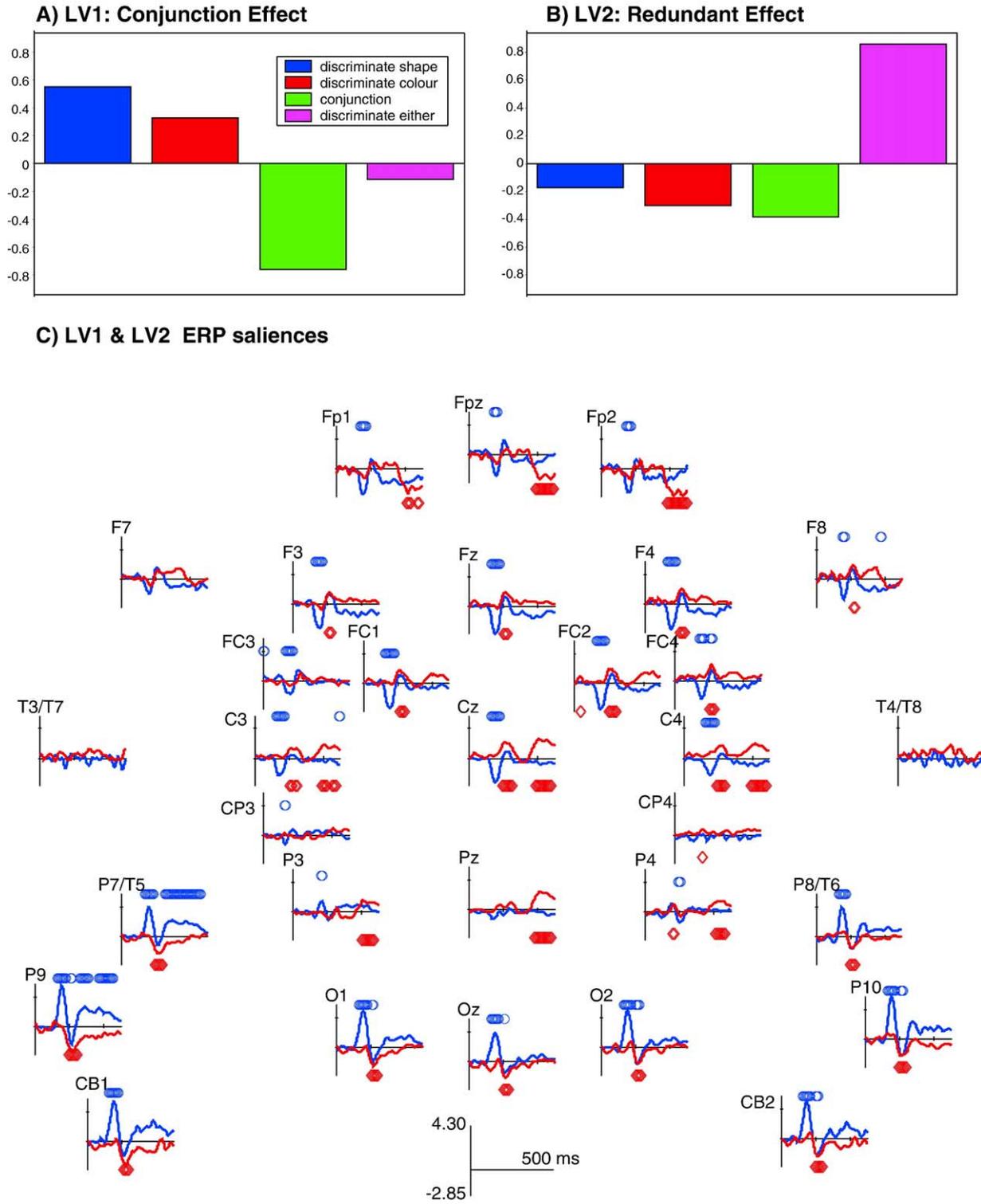


Fig. 2. TaskPLS results. (A) Contrast identified on the first latent variable. The conditions with negative weights (conjunction, redundant) differed from those with positive weights (shape, color). The largest difference was between conjunction targets and discriminate shape targets. (B) Contrast identified on the second latent variable. The conditions with negative weights (shape, color, conjunction) differed from the redundant targets. (C) Electrode saliences for all electrodes. Blue = LV1, Red = LV2. Blue markers at the top and red markers at the bottom of each plot indicate saliences stable by bootstrap estimation.

To summarize the PLS data, “ERPscores” can be calculated for each LV (Lobaugh et al., 2001; McIntosh and Lobaugh, 2004). These are similar to factor scores and reflect the degree to which each subject expresses the task–ERP relation or the RT–ERP relation. These are the dot product of the saliences and the original data matrix, providing a single value for each subject. In the case of the BehaviorPLS, the correlation of the ERPscores with RT for each condition provides a pattern of correlations similar to the pattern expressed by the behavior saliences (e.g., Fig. 5). It is these correlations that are assessed by the bootstrap resampling.

As a complement to the PLS analyses, classical peak analyses of ERP latency and amplitude data were conducted on the P1 and N1 components at four posterior electrode pairs (O1/O2, P7/P8, P9/P10, CB1/CB2). P1 and N1 data and reaction times (RT) for targets and nontargets were assessed with repeated-measures analyses of variance (with Greenhouse–Geisser adjusted degrees of freedom). Post hoc Newman–Keuls tests were conducted on significant interactions.

Results

Behavior

As is typical when nontargets are more frequent than targets, nontarget RTs were faster than target RTs ($F(1,28) = 31.02, P < 0.001$; Table 1). A Task \times Target interaction ($F(2.50, 69.89) = 5.89, P < 0.002$) indicated that target RTs were fastest for targets in the single-feature shape discrimination task. Accuracy was high (>93%) for all trial types.

TaskPLS results

Two of the three TaskPLS latent variables were significant (LVs 1 and 2, $P_s = 0.001$; LV3, $P = 0.510$). The first latent variable identified accelerated and amplified neural processing to conjunction targets. The second pattern identified differences between the redundant targets and the other three target types. As there was

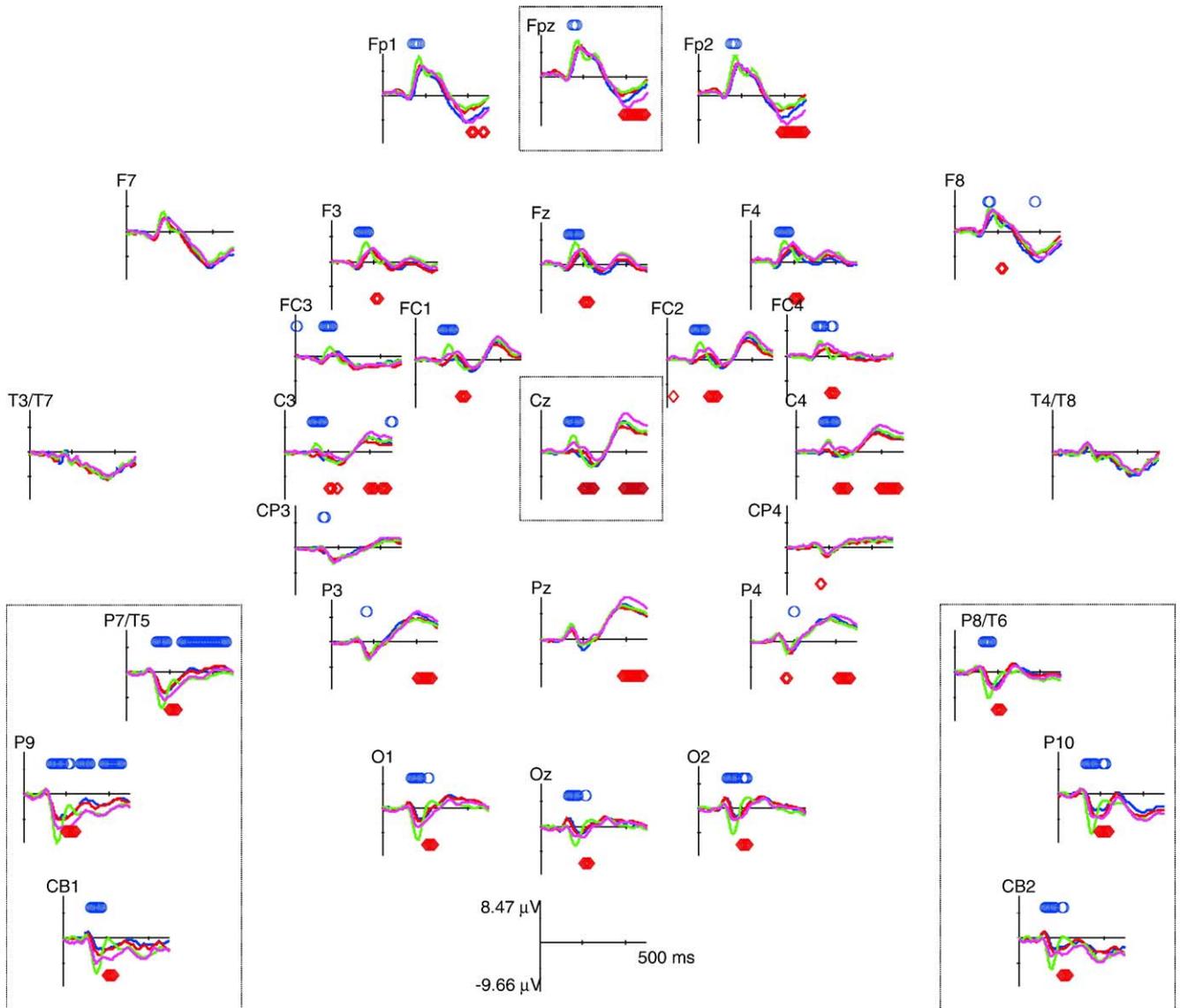


Fig. 3. Grand averaged ERPs for all tasks. Blue = discriminate shape; Red = discriminate color; Green = conjunction; Magenta = redundant (discriminate either). Markers at the top and bottom of each plot are the same as in Fig. 2C. Note the much larger response to conjunction targets at the N1 (P9/P10) and at frontal electrodes. Channels highlighted by the dotted line boxes are shown in more detail in Fig. 4.

some overlap in the spatiotemporal expression of these two sets of ERP differences, the ERP saliences for LV1 and LV2 are shown together in Fig. 2.

LV1: conjunction effect

For LV1, the design saliences (Fig. 2A) indicated that conjunction targets differed most strongly from the two single-feature targets (shape and color). The largest difference was between the conjunction and discriminate shape targets. The electrode saliences are shown in Fig. 2C (blue lines) with time points with stable differences indicated by blue markers above each plot. The electrode saliences are interpreted as follows: positive saliences indicate time points where the ERP ampli-

tudes were more negative for the conjunction targets with respect to the other conditions, and especially with respect to the discriminate shape targets; negative saliences indicate time points where ERP amplitudes were more positive for the conjunction targets. Differences between conjunction targets and the other conditions were found over posterior and frontal cortices starting as early as 125 ms after stimulus onset. This effect was strongest (largest saliences) over a broadly distributed set of posterior channels and lasted until approximately 200 ms (e.g., positive saliences at P9/P10; CB1/CB2; O1/O2). The conjunction effect was weaker, but stable, over frontal electrodes (Fp1/Fpz/Fp2). After a brief transition period, differences then emerged as a more constrained bilateral distribution over

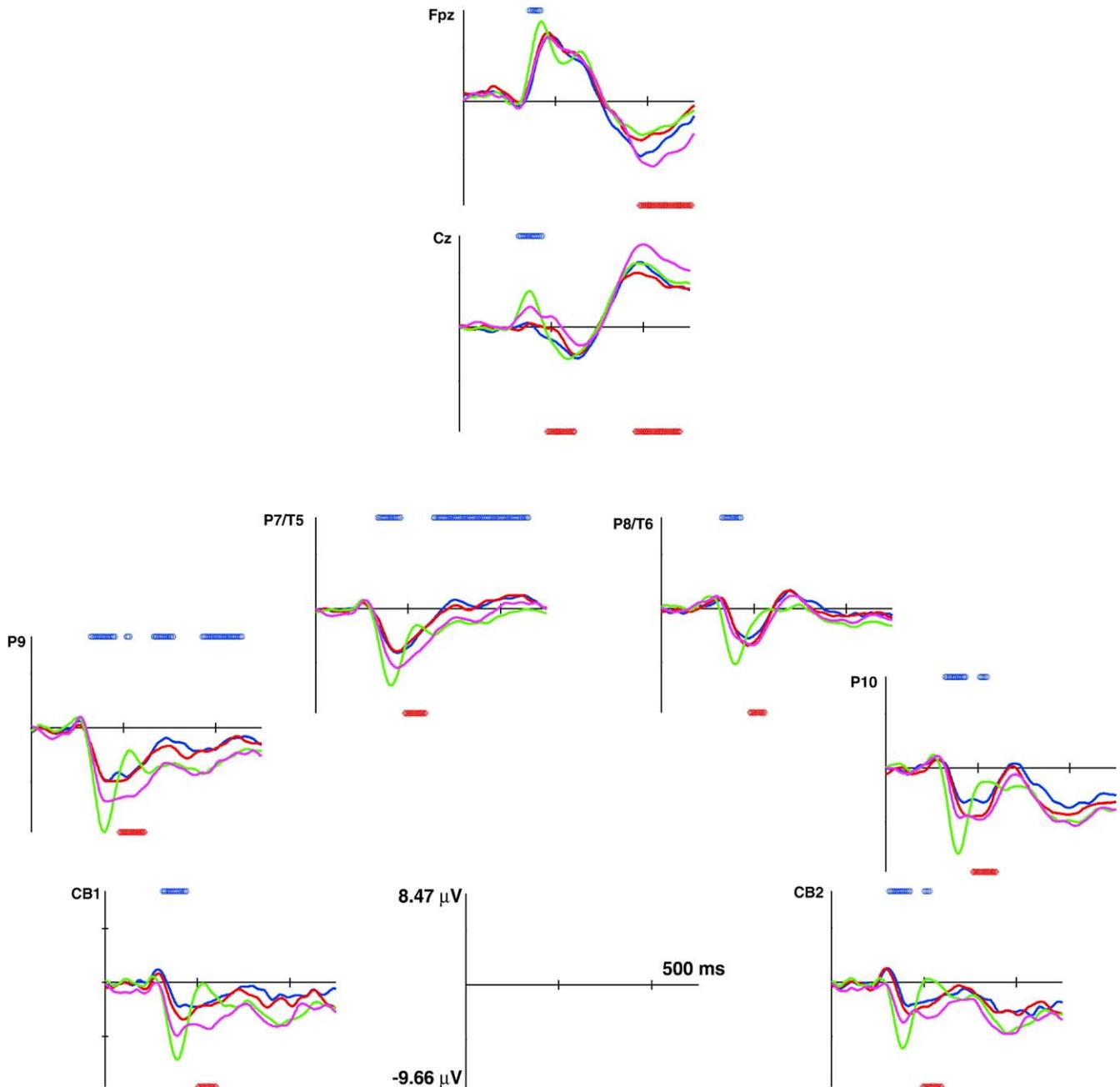


Fig. 4. Grand averaged ERPs for posterior, central, and frontal electrodes. Line colors as in Fig 3, markers as in Fig. 2.

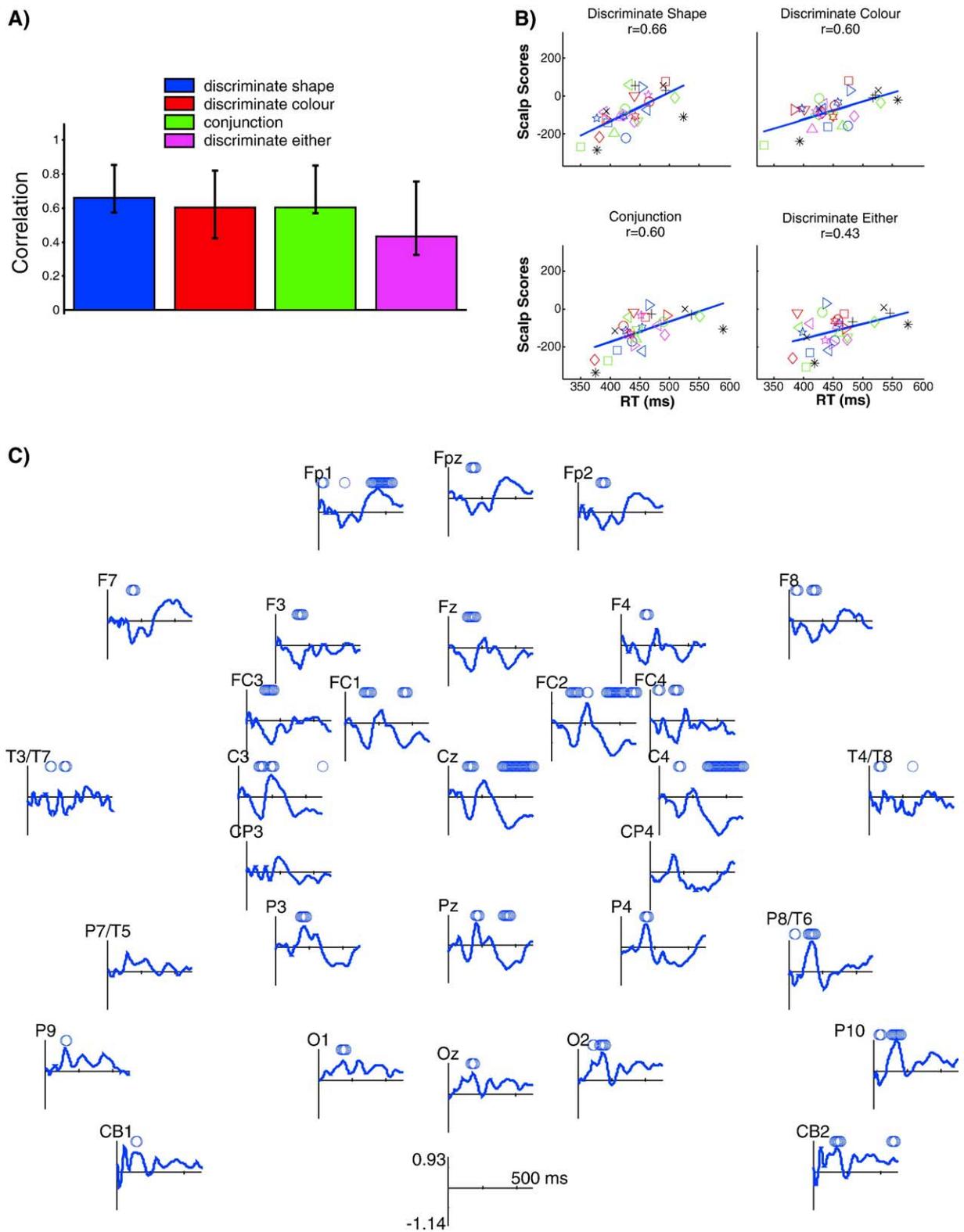


Fig. 5. BehaviorPLS results. (A) Correlations of reaction time with ERP amplitude. The correlation of scalp scores with RT is plotted. Error bars indicate the upper and lower limits of the 95th percentile confidence interval around the correlation. (B) Scatterplots of scalp scores and RT (ms) in each condition. Line of best fit is shown in each plot. (C) Electrode saliences for all electrodes. Markers at the top of each plot indicate saliences stable by bootstrap estimation. Where saliences are positive, more positive ERP amplitudes were related to slower RTs, where saliences are negative, more positive ERP amplitudes were related to faster RTs. A combination of effects at two intervals and topographies contributed to fast RTs: RTs tended to be faster if ERP amplitudes were more negative at right posterior electrodes (P8, P10, O2, CB2) and were more positive at central electrodes after 300 ms. (This late effect was inverted at left frontal leads.)

parieto-occipital sites from 200 to 300 ms (negative saliences: P9/P10, O1/O2), followed by sustained differences from 300 to 500 ms over left posterior parietal sites (e.g., P7, P9).

LV2: redundant effect

The LV2 design saliences (Fig. 2B) indicate that the primary effect on this latent variable was between the redundant target and the other three target types. The early part of this effect was also seen over posterior channels (P7/P8, P9/P10, CB1/CB2), but was much later than the conjunction effect, encompassing an interval from ~190 to 240 ms. Strong saliences were also seen starting at ~370 ms at central and frontal electrodes (Cz, C3/C4, FPz).

ERP results

The ERP waveforms indicate whether the maximal electrode saliences are identifying differences in peak amplitudes, latency shifts, or differences during peak transitions. The ERPs for the full dataset are shown in Fig. 3 and for selected channels in Fig. 4. Time points of stable differences are indicated as in Fig. 2. These are described in detail below.

LV1. Conjunction-effect ERPs

The first stable differences were found just after the peak of the P1 component for the conjunction targets (~125 ms). After this, salience strength increased (Fig. 2C). The ERPs showed that these strong posterior saliences identified a large, fast N1 component, which was especially prominent at P9/P10 (Figs. 3 and 4). The design saliences (Fig. 2A) indicate that the redundant task was intermediate to the conjunction and single-feature targets. This is clearly seen at the latency of the N1 as well: redundant target amplitudes were in-between the conjunction and single-feature amplitudes. The enhanced early processing is also seen inverted at frontal electrodes (e.g., FP1/FPz/FP2, Fig. 3). The saliences also indicated the conjunction (and redundant) targets differed from the other targets over left parietal electrodes (P7/P9) at later time points, as seen in the sustained negativity after 250 ms.

LV2. Redundant-effect ERPs

All single-feature targets showed a broader N1 compared to the conjunction targets. The redundant targets differed from the single-feature targets in that the N1 was more negative not only at the peak of the N1, but this negativity was more sustained, lasting up to ~250 ms (e.g., P9, CB1). The strongest amplitude difference (largest saliences) between the redundant and other targets was seen at the latency of the P3 component (around 400 ms), where redundant P3s were larger than all other targets.

ERP latency and amplitude results

The findings of an amplified and accelerated N1 for conjunction targets were confirmed by repeated-measures ANOVAs on peak amplitudes and latencies (Table 1). The P1 to the conjunction and redundant targets was faster than the other conditions. The fastest and largest N1s were seen for conjunction targets. Thus, when subjects had to use a conjunction of features to identify the target, this was done significantly faster (10–15 ms) than processing single-feature targets; a substantial facilitatory effect.

RT–ERP correlations

One latent variable from the BehaviorPLS analysis was significant ($P = 0.001$). The RT–ERP correlations were equally strong in all conditions ($r = +0.43$ to $+0.66$; Fig. 5A), indicating that across the scalp the shortest latency RTs were accompanied by the smallest (most negative) ERP amplitudes. These correlations are shown as scatterplots of scalp scores with RT in Fig. 5B. Electrode saliences, indicating the spatiotemporal expression of this correlation, are shown in Fig. 5C. Positive saliences (e.g., P8, P10) show time points where the RT–ERP correlation was positive: fast RTs were associated with more negative ERP amplitudes. Negative saliences (e.g., Cz, FC2) show time points where the RT–ERP correlation was negative: fast RTs were associated with larger ERP amplitudes. The topography of the saliences indicated strong involvement at temporo-parieto-occipital electrodes in the 100- to 200-ms interval, especially in the right hemisphere (e.g., P8, P10), with the early negative frontal correlations being polarity reversals of this effect. The early correlations were followed by sustained correlations at centro-frontal electrodes after 300 ms (e.g., Cz, C4, FC2). Scatterplots of RT with ERP amplitudes are shown Fig. 6 for P10 at the peak of the positive RT–ERP correlations (132 ms) and for Cz at the

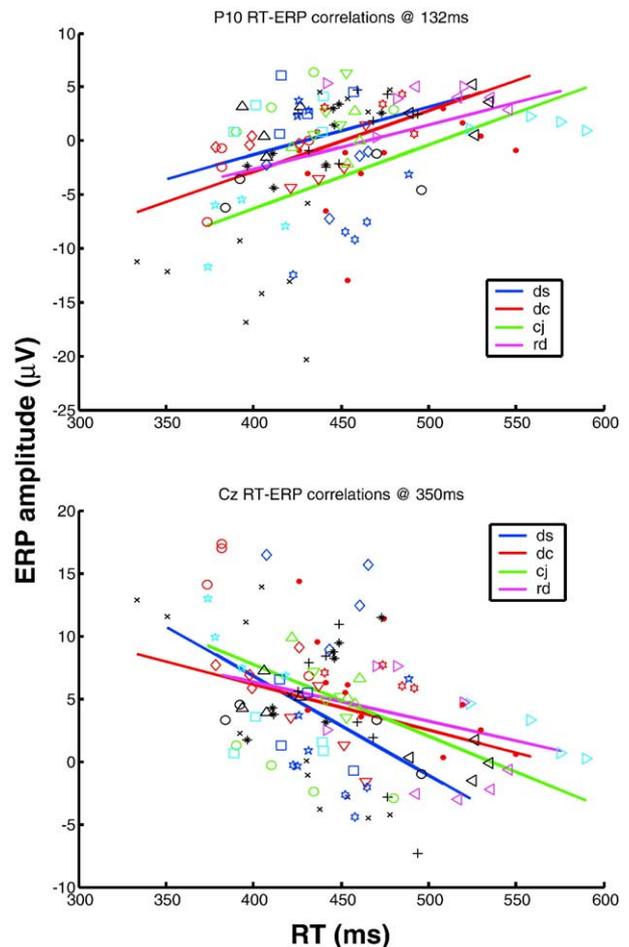


Fig. 6. RT–ERP correlations. RT–ERP scatterplots for each condition at the point of maximal saliences for P10 (132 ms, top) and Cz (350 ms, bottom). The color–symbol combinations reflect the four tasks for each of the 29 subjects. Linear fits are also plotted, highlighting the similar correlations across conditions.

peak of the negative RT–ERP correlations (350 ms). Thus, the fastest RTs in each condition were seen when the transition from the P1 to the N1 component was fast and more negative, followed by larger P300 amplitudes at central electrodes, and smaller long-latency (300–420 ms) amplitudes at frontal electrodes. Correlations of P300 amplitudes with behavior are classic (Kutas et al., 1977); what is new here is the finding that early peak amplitudes combine with P300 amplitudes to predict fast responding.

Discussion

ERPs are ideal for discriminating the earliest stages of neural processing in humans, and there is recent ERP evidence for rapid, integrated processing, both within and between modalities (Fort et al., 2002; Giard and Peronnet, 1999; Molholm et al., 2002; Taylor, 2002). ERP studies have also shown the response to feature conjunctions can occur at the same latency as the response to single features (Cortese et al., 1999; Theunissen et al., 2001), suggesting the separate features are processed in parallel. Additionally, a few studies have reported enhanced responses to conjunction targets, seen as larger ERP amplitudes (Woods and Alain, 2001). It is important to note, however, that these effects are not typically seen in studies using visual arrays (Woodman and Luck, 1999). Here, we provide evidence not only of amplification, but also of accelerated early cortical processing when task demands are increased by the requirement to conjoin features. As only correct trials were averaged, the conjunction target ERPs reflect the rapid and accurate binding of two features.

The task demands also produced interesting correlations between behavioral and ERP data. The BehaviorPLS results indicated that N1 and P300 amplitudes were correlated with RT in all task conditions. This added influence of the short-latency visual N1 responses on speed of reaction time is a novel finding. To illustrate this point, we divided the subjects into fast and slow responders based on mean RT across all target conditions. The combined effects of conjunction-target ERP facilitation and RT–ERP correlations are shown in Fig. 7, where mean ERPs for conjunction and “discriminate shape” targets are presented for these two subsets of subjects. At P9, only TaskPLS conjunction effects were strong, while at Cz, only BehaviorPLS effects were evident for the P3. At P10, both BehaviorPLS and TaskPLS indicated involvement of the N1. These separate and combined effects are clearly seen in the ERPs. ERPs at P9 reflect primarily the conjunction facilitation effect seen in the TaskPLS. At Cz, P3 amplitudes reflect RT differences seen in the BehaviorPLS: fast responders had larger P3s than slow responders. The conjunction facilitation effect at P10 was stronger in fast responders (red arrows) compared to slower responders (black arrows), mapping onto the combined TaskPLS and BehaviorPLS findings. These results extend to humans the findings from primate electrophysiology which have shown enhanced responses in visual cortices related to faster RTs (Lee et al., 2002; Supèr et al., 2003), and suggest the right hemisphere is particularly implicated in this type of task.

The combination of strong N1–RT correlations and facilitated N1 response to conjunction targets argues against hierarchical models of visual processing. This is probably due, in part, to the fact that target and nontarget stimuli were presented serially at one location. PLS also identified a long-latency sustained left posterior activity (perhaps the activity reflected in fMRI studies of feature

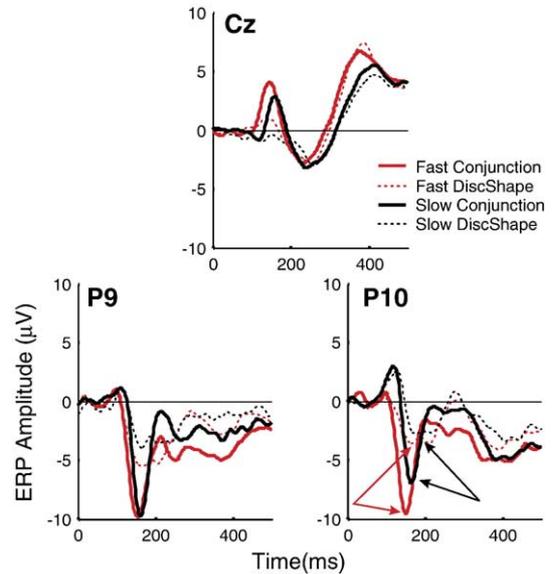


Fig. 7. ERP amplitude and RT. Grand averaged ERPs for conjunction (solid lines) and single-feature discriminate shape targets (dotted lines) for fast (red lines) and slow (black lines) responders. As was indicated by the TaskPLS and BehaviorPLS results, fast responders show both an accelerated and facilitated N1 and a larger P300. Arrows in the P10 plot highlight the larger N1 conjunction facilitation effect for fast compared to slow responders.

binding (Nobre et al., 2003)) that was most negative for the conjunction and redundant targets. As this activity was not directly related to behavior, it is not clear what the role of this additional activity is.

Redundant targets shared some processing features with the conjunction targets. The amplitudes at the latency of the N1 were intermediate between the conjunction and “true” single-feature tasks, suggestive of a smaller N1 facilitation effect for these stimuli. The broad response after the peak of the N1, however, was more similar to the other single-feature stimuli, although more negative. One possible explanation for this apparent mix of processing differences would be that subjects may have maintained a conjunction processing “set” for some trials in the redundant task. Deficits in switching back to a simple single-feature strategy is thought to underlie reaction-time variability in neurologically impaired subjects (Stuss et al., 1994). Tests of this hypothesis would require the ability to classify individual trials, which would involve a substantially larger number of target trials and single-subject/single-trial analyses (e.g., Jung et al., 2001).

The speed with which the visual system processes simple as well as complex stimuli has been increasingly investigated in recent years in both human and animal models, with the demonstrated speed of processing increasing dramatically (Bullier, 2001; Foxe and Simpson, 2002). The short-latency P1 and N1 ERP components have been shown to index attention to visual stimulus features (Anillo-Vento et al., 1998; Han et al., 2000; Taylor, 2002), and the present results indicate attentional effects on discriminative processing were seen starting at the P1 (Table 1, TaskPLS). P1 latencies to conjunction targets were among the fastest, suggesting rapid global visual processing (Taylor, 2002), and pushing forward the timing for processing differences from what is often reported in the literature (Hopf et al., 2002). By the N1 latency, sufficient processing had occurred that single feature and conjunction targets

had distinct amplitudes as well as latencies. Thus, these data demonstrate the human visual system is able to conjoin features rapidly, accelerating and amplifying the processing of relevant stimulus dimensions.

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