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Cortical mechanisms of attention in time: neural correlates of the Lag-1-sparing phenomenon

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Abstract

If humans monitor streams of rapidly presented (≈ 100-ms intervals) visual stimuli, which are typically specific single letters of the alphabet, for two targets (T1 and T2), they often miss T2 if it follows T1 within an interval of 200–500 ms. If T2 follows T1 directly (within 100 ms; described as occurring at 'Lag 1'), however, performance is often excellent: the so-called 'Lag-1 sparing' phenomenon. Lag-1 sparing might result from the integration of the two targets into the same 'event representation', which fits with the observation that sparing is often accompanied by a loss of T1–T2 order information. Alternatively, this might point to competition between the two targets (implying a trade-off between performance on T1 and T2) and Lag-1 sparing might solely emerge from conditional data analysis (i.e. T2 performance given T1 correct). We investigated the neural correlates of Lag-1 sparing by carrying out magnetoencephalography (MEG) recordings during an attentional blink (AB) task, by presenting two targets with a temporal lag of either 1 or 2 and, in the case of Lag 2, with a nontarget or a blank intervening between T1 and T2. In contrast to Lag 2, where two distinct neural responses were observed, at Lag 1 the two targets produced one common neural response in the left temporo-parieto-frontal (TPF) area but not in the right TPF or prefrontal areas. We discuss the implications of this result with respect to competition and integration hypotheses, and with respect to the different functional roles of the cortical areas considered. We suggest that more than one target can be identified in parallel in left TPF, at least in the absence of intervening nontarget information (i.e. masks), yet identified targets are processed and consolidated as two separate events by other cortical areas (right TPF and PFC, respectively).

Introduction

Parallel distributed systems such as the human brain seem to be able to achieve robust representations of the perceptual world by the concerted interaction of billions of neurons. As robustness increases with processing time, speed and robustness can be regarded as antagonistic constraints, which raises the important question of how attentional top-down control might flexibly moderate this conflict. The so-called 'attentional blink' (AB) phenomenon (Raymond *et al*., 1992) has proven to be of great utility in this context as it affords an opportunity to study the role of attention in processing perceptual input over time.

The AB effect is revealed if two to-be-identified targets appear in quick succession (stimulus onset asynchrony or SOA < 500msec) within a rapid serial visual presentation (RSVP) stream (Raymond *et al*., 1992) or if they are properly pattern-masked (Duncan *et al*., 1994). The effect is defined by a dramatic drop in performance on the second target (T2) at a maximum ≈ 300 ms SOA, apparently due to processes triggered by the first target, T1 (Raymond *et al*., 1992). However, a robust drop in performance only occurs if both T1 and T2 are masked effectively, whether by the items which follow them in the stimulus stream in which the targets are contained (Raymond *et al*., 1992; Chun & Potter, 1995; Grandison *et al*., 1997; Seiffert & Di Lollo, 1997; Giesbrecht & Di Lollo, 1998; Brehaut *et al*., 1999) or by individual, irrelevant symbols or patterns (Duncan *et al*., 1994).

A theoretically interesting exception occurs if the first target is directly followed by the second, that is, with a temporal lag of 1. In this case the processing of the two targets is not disrupted by an intervening mask (the mask actually seems to cause the AB) so performance often reaches the baseline level obtained with detection and identification of single targets, i.e. is markedly good [provided that no substantial task-set switch is required in between the two targets; Visser, Bischof & DiLollo (1999) report a metaanalysis of 111 AB experiments and suggest that the occurrence of Lag-1 sparing might depend on the complexity of the task-set switch from T1 to T2, that is, if T1 and T2 differ in location and/or on more than one dimension (e.g. task and category) then Lag-1 sparing is likely to disappear.] We hypothesize that (at least) two, not mutually exclusive, processes could occur. First, the two temporally adjacent targets may compete for access to attentional resources at the level of identification (Potter *et al*., 2002, 2005; Hommel & Akyürek, 2005), so that gains for T2 would come with losses for T1. Indeed, a trade-off between the two targets at Lag 1 has been repeatedly observed (Potter *et al*., 2002, 2005; Hommel & Akyürek, 2005). Second, the temporal proximity of the two targets may cause their integration into a single episode (Shapiro *et al*., 1994; Chun & Potter, 1995), which is consistent with the observation that information about the temporal order of the two targets is often lost for Lag 1 (Shapiro *et al*., 1994; Chun & Potter, 1995).

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To get more insight into the processes underlying Lag-1 sparing we took a neurophysiological approach and recorded brain activity using a 122-channel whole-head neuromagnetometer (Neuromag$^{\text{TM.}}$) during a task that was likely to produce the sparing phenomenon. We focused on the M300, a modulation of the magnetic evoked responses ≈ 300 ms after stimulus onset (the magnetic counterpart of the electric P300), as this component has been linked to stimulus-related working memory updating in general and found to be attenuated during the AB effect in particular (Vogel *et al.*, 1998; McArthur *et al.*, 1999; Vogel & Luck, 2002; Kranczioch *et al.*, 2003; Arnell *et al.*, 2004). Although variations in amplitude have been primarily reported for the P300 in various cognitive paradigms, Vogel & Luck (2002) and Arnell *et al.* (2004) have found variations in P300 peak latencies to be affected during the AB. We therefore considered amplitudes and latencies of the M300, which was studied in three broadly defined cortical clusters that have previously been identified as the main components of the attentional network involved in the AB (Gross *et al.*, 2004): a prefrontal cluster and a left and right temporo-parieto-frontal (TPF) cluster.

Although it is difficult to translate the available cognitive models into concrete neurophysiological predictions, we were particularly interested in two potential data patterns which could be viewed as support for their respective hypotheses. First, an important implication of the competition model (Potter *et al.*, 2002, 2005) is that at very short SOAs T2 is likely to be processed prior to T1 (Potter *et al.*, 2005). Usually this occurs only at SOAs < 100 ms, so we did not expect to observe this effect with an SOA of 100 ms at Lag 1. With such an SOA the early competition hypothesis suggests delays in the M300, that is, a later-peaking M300 for temporally close (and, hence, competing) targets in the cortical cluster that is related to the hypothetical processing bottleneck. In addition, amplitudes of the M300 might be reduced due to competition. Alternatively, the integration hypothesis suggests a single M300 component if the two targets appear in close succession. That is, integrating two targets into a single episode may merge the related M300 responses, especially in the clusters where integration and consolidation take place. As an important control, we also employed a Lag-2 condition without a T1 mask to determine whether integration could survive a longer T1–T2 SOA (200 ms), thus potentially accounting for the preserved performance, i.e. Lag-1 sparing, under such conditions (Raymond *et al.*, 1992; Grandison *et al.*, 1997; Giesbrecht & Di Lollo, 1998; Visser *et al.*, 1999).

Materials and methods

Subjects and experimental procedure

Subjects were right-handed, four being members of the University staff and six being students at Duesseldorf University. Mean ± SD age was 28.8 ± 5.8 years); three were female and seven male. Individuals had no neurological deficits and gave their written informed consent prior to the experiment. The study was approved by the local ethics committee and is in accordance with the declaration of Helsinki.

We have adopted the simplified version of the AB task introduced by Duncan and colleagues (Duncan *et al.*, 1994; Ward *et al.*, 1997) as shown in Fig. 1 and combined three independent variables in a repeated-measures design. Factors were 'lag' (1 or 2), 'number of targets' (zero, one or two targets present), and 'masking' with respect to the first target (masked or unmasked). The factors 'lag' and 'masking' were not entirely independent: at Lag 1, T1 was followed by T2, so masked vs. unmasked T1 was not applicable for this lag. We therefore analysed the impact of lag and masking separately. The dependent variables were the percentage of correct target identifications in single-target trials and the percentage of correct T2 identifications given T1 correct identification (T2|T1) in dual target trials, as is conventional for AB analysis. In addition we provide an unconditionalized report of types of behavioural outcomes (in percentages) for all three dual-target conditions.

The experiment consisted of 12–16 blocks per subject containing 260 trials each. The number of blocks was increased until the respective subject reached at least 90 trials in each condition of interest in order to achieve a good signal-to-noise ratio (note that the number of 'AB' vs. 'noAB' trials depended on the performance on both targets of the respective subject). An additional block of 24 trials was used at the start of the experiment for instruction of the subject and for practice. Target letters were restricted to 'X' and 'O', while masks could be any other letter of the alphabet. Each letter was on screen for 50 ms and was followed by a blank screen of 50 ms. As can be seen in Table 1, when two targets were presented, T1 always occupied the first position in the stream. T2 was presented either immediately after T1 (at Lag 1, SOA 100 ms, interstimulus interval 50 ms) or with an SOA of 200 ms (at Lag 2). In the latter case there were two possibilities: first, another letter of the alphabet could intervene between T1 and T2 (masked T1 condition) or, second, there was a gap between T1 and T2 of 150 ms interstimulus interval (unmasked T1 condition). A target in single-target trials could appear in any of the first three positions of the stream. Note that there were also single-target trials where a gap of

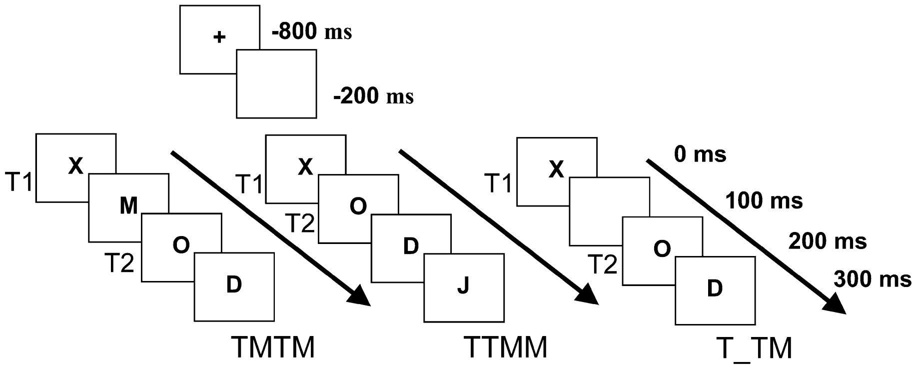


FIG. 1. The experimental procedure. The figure shows all three possible dual-target conditions. In TMTM, T1 was followed by a masking letter while in T_TM a gap was inserted between T1 and T2. In TTMM, T1 was immediately followed by T2. The time stamps in the figure refer to the onset time of each letter in the stream (time 0 is defined as the onset of the first letter). Each letter was on screen for 50 ms followed by a blank screen of 50 ms. After the last letter in the stream a blank screen was presented for 650 ms, followed by the request to report the number and the identity of the targets spotted in the stream.

TABLE 1. Conditions employed in the experiment

Conditions	*n*
Single target	
T_MM	20
TMMM	20
MTMM	20
MMTM	20
Dual target	
T_TM	40
TMTM	40
TTMM	40
Masks only	
MMMM	40
M_MM	20

The conditions are labelled according to the qualities of the letter stream that was used. A ‘T’ denotes a target (‘X’ or ‘O’) at a certain stream position while ‘M’ stands for mask, i.e. nontarget letters. Underscores (‘_’) signify blank gaps in the stream. For example the letter stream ‘X’, ‘B’, ‘O’, ‘S’ is labelled as ‘TMTM’. *n*, denotes the number of trials for each condition in each block. There were 260 trials in each block.

150 ms followed the target (thus replacing the second item), which was always at position 1 in order to parallel the dual target condition and thus prevent predictability (see Table 1). On a third of all pure mask trials an identical gap after the first letter was included as well to reduce predictability. In summary, all trials consisted of either three or four letters, while the end of each stream occurred fixed at 350 ms after the appearance of the first letter as the ‘missing’ letter was always at position 2 (see Table 1).

Letters were presented on a back-projection screen with a visual angle of 3.72° at a distance of 1.2 m. Behavioural responses were collected using the following procedure. Subjects had three buttons to press, one each for the right thumb, index finger and middle finger; they initiated each trial in a self-paced manner by pressing the right thumb button. After presentation of the letter stream, a display was shown instructing the subject to give one of the following responses. If zero, one or two targets were detected, the subject was to respond by pressing a button with the thumb, the right index finger or the right middle finger, respectively. In the case where one or two targets were indicated, a second display was shown. In the case of a single target, subjects were instructed to indicate its identity (‘X’ by pressing the right index or ‘O’ by pressing the right middle finger). In the case of two targets, the subject was instructed to indicate the order of the targets (‘X–O’ by pressing the right index or ‘O–X’ by pressing the right middle finger). A subsequent display indicated that the subject could initiate the next trial by pushing the thumb button again. After each block of trials, which took ≈ 15 min, subjects were asked whether they wanted a short (≈ 3-min) or a long (≈ 10-min) break. Usually subjects preferred a sequence of two short breaks and then a longer break after the next block. In the middle of the experiment (after ≈ 6–8 blocks) subjects received a longer break of at least 30 min.

Magnetoencephalography (MEG) measurement

Using a 122-channel whole-head neuromagnetometer (Ahonen *et al*., 1993), brain activity was recorded with a band-pass filter of 0.03–170 Hz and digitized at 514 Hz. Vertical electro-oculogram was recorded simultaneously for off-line rejection of epochs contaminated by eye movements and eye blinks. MEG signals were averaged off-line between −500 and +1000 ms with respect to the letter stream onset.

The process of source modelling consists of continuous interplay between inspection of coherent local signal variations in the original responses, search for clear dipolar field patterns in the analysis program, dipole modelling and evaluation of the fitted dipoles (Hämäläinen *et al*., 1993). The channel with the largest peak and the surrounding 8–10 channel pairs were selected for dipole modelling. Only sources with a goodness-of-fit of > 85% were accepted. The current dipoles were identified one-by-one, at time points where each specific field pattern was clearest. The sources were then brought into a multidipole model where the source locations and orientations were kept fixed, whereas their amplitudes were allowed to vary as a function of time to best account for the signals measured by all 122 sensors in all experimental conditions. Note that only one model was obtained that explained the measured signals in all experimental conditions. Figure 2 provides a sample of eight sensors for which the modelled signal (grey line) is compared to the actually measured signal (black line) in a single subject.

The resulting source waveforms represent the time courses of activation in the cortical source areas. The complete models included 7–10 sources per subject. The location of each source is defined in head coordinates, set by clearly identifiable points in front of the ear canals (*x*-axis, from left to right) and by the nasion (positive *y*-axis); the *z*-axis is orientated towards the vertex. The position of the head within the magnetometer was found by attaching four small coils to the subject’s head, measuring their location in the head coordinate system with a 3-D digitiser (Isotrak 3S1002, Polhemus Navigation Sciences) outside the MEG system, and energizing them briefly, inside the MEG system, to obtain their locations in the magnetometer coordinate system. MEG sources were combined with the individual anatomy by marking the three anatomical points in the individual magnetic resonance images. In a further step individual source locations were mapped onto a standard brain by using SPM99 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London). For further analysis of the waveforms we extracted four clusters of cortical sources (dipoles), with one source per subject being included in each cluster. There was an occipital (dipoles fitted individually within 79–159 ms after stream onset), a right TPF (dipoles fitted individually within 177–287 ms after stream onset), a left TPF (dipoles fitted individually within 303–391 ms after stream onset) and a prefrontal (dipoles fitted either within 284–395 ms or 547–593 ms after stream onset) cluster.

The extrastriate source locations, especially in the right TPF cluster, were quite distributed across individuals and covered a wide range of temporal, parietal and frontal areas. This is in concordance with the modelling results from one of our MEG pilot studies and with other findings that show a wide range of areas being involved in processing of dual target RSVP tasks (Marois *et al*., 2000; Feinstein *et al*., 2004; Gross *et al*., 2004). We interpret this as a symptom of the very complex and intermixed cognitive processes involved in the AB: quite large networks are involved in some subprocesses and different components might be best to trace in each individual with the method of dipole modelling. This method assumes cortical sources with practically no spatial extension yet with a high variability in activation over time in contrast to more widespread and slowly activated volumes such as the ones obtained with imaging techniques. As we were primarily interested in the M300 components and their temporal variations, dipole modelling was the method of choice. We therefore traded anatomical correspondence between individual sources for the similarity of their waveform signals. That is, clusters were determined by a rough anatomical classification in a left and a right TPF cluster but most importantly by the temporal similarity of signal properties across the subject’s multidipole models. Hence, those sources were

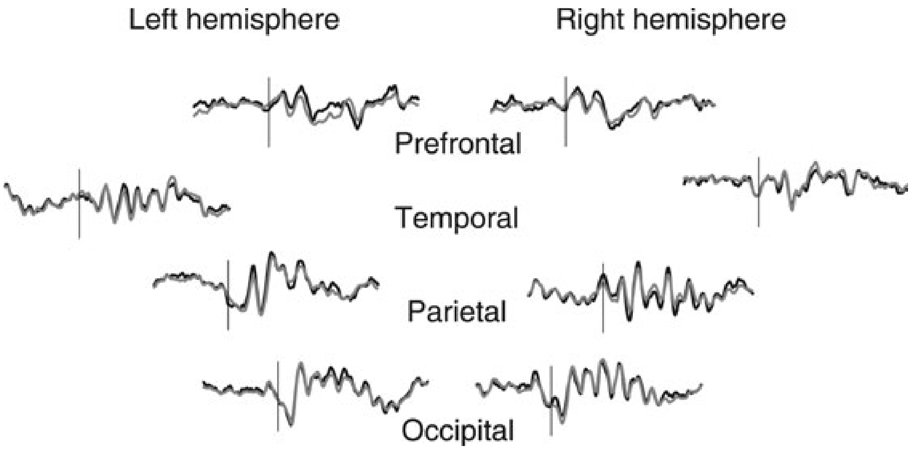


FIG. 2. Match between measured and modelled signals in a single subject. Eight MEG signals are shown; the sensors were located over distinct parts of the brain (left and right occipital, parietal, temporal and prefrontal sensors). The grey line denotes the signal derived from the multidipole model for each sensor. This modelled signal is contrasted to the actually measured signal at each sensor, shown by the black line. The example shows measured and modelled signals from the T1-masked dual target condition.

clustered together (one source from each subject) that showed minimal interindividual variability over time (as an objective criterion the average of the SEM was computed and minimized across the trial interval).

As pointed out, our main focus of interest was directed towards the M300 components that have been related to the AB (analogous to the P300 component in the EEG). Therefore, we identified by means of automatic peak detection the peaks for each subject for each source in each extrastriate cluster that lay within a time window of 250–450 ms after target onset. Consequently, for targets occurring at stream positions 2 and 3 the onset delay was added to the interval, resulting in a time window of 350–550 ms after stream onset for targets at position 2 and of 450–650 ms for position 3. As these time windows overlap for Lag-1 trials, it was possible that the same peak was identified for both time windows. On trials when this occurred, the windows were narrowed down sample-by-sample until two distinct peaks were identified, i.e. one for each time window. Amplitudes and latencies were thus quantified for each source. In the occipital and the right TPF cluster, cortical responses were biphasic in that a positive peak was followed by a negative peak. To account for modulations on both components peak-to-peak measures were employed as quantification for amplitudes. Means and SDs for each source cluster and condition are provided in Table 2. As subjects differed substantially in the strength of their cortical responses, nonparametric Wilcoxon tests (two-tailed) were used to determine differences in amplitude between conditions. In contrast, latency differences between conditions were analysed with paired *t*-tests because interindividual time scales were similar.

Note that there is a substantial difference between the usually reported P300 in the EEG and the M300s analysed here. The M300 waveforms were drawn from individual sources (and then averaged) while the P300 is usually analysed at the electrode level. Hence, despite interindividual variability in the exact source locations within the clusters, each source waveform represents a signal where the influences of the other sources (of this individual) have been filtered out. In contrast, at the electrode level the signal from a broad range of

TABLE 2. M300 peaks

RSVP stream	S_1			S_2			S_3		
	CS	Time	Amplitude	CS	Time	Amplitude	CS	Time	Amplitude
PFC: M300 peaks for T1 and T2; grey bars 1 and 2 (Lag 1) and 1 and 3 (Lag 2) respectively in Fig. 5									
$T_1M_1T_2M_2$	T_1	320.81 ± 42.74	1.92 ± 1.07				T_2	565.23 ± 19.31	1.76 ± 1.39
$T_1T_2M_1M_2$	T_1	328.05 ± 34.16	2.02 ± 1.65	T_1	449.87 ± 31.30	1.45 ± 1.75			
T_1_T_2M_1	T_1	354.70 ± 43.79	1.70 ± 1.02				T_2	534.77 ± 28.02	1.84 ± 1.24
$M_1M_2M_3M_4$	M_1	328.48 ± 55.98	0.82 ± 0.72	M_2	449.49 ± 37.05	0.43 ± 0.69	M_3	533.25 ± 45.80	0.56 ± 0.73
Right TPF: M300 peaks for T1 and T2; grey bars 1 and 2 (Lag 1) and 1 and 3 (Lag 2) respectively in Fig. 6									
$T_1M_1T_2M_2$	T_1	359.69 ± 29.81	2.51 ± 1.53				T_2	548.14 ± 29.66	1.35 ± 0.92
$T_1T_2M_1M_2$	T_1	331.95± 33.08	2.82 ± 2.19	T_1	461.89 ± 32.31	1.99 ± 1.58			
T_1_T_2M_1	T_1	358.55 ± 27.23	2.99 ± 2.06				T_2	533.63 ± 44.66	1.42 ± 0.83
$M_1M_2M_3M_4$	M_1	364.62 ± 31.18	1.92 ± 1.57	M_2	459.61 ± 31.44	1.17 ± 0.80	M_3	557.23 ± 36.65	0.89 ± 0.70
Left TPF: M300 peaks for T1 (grey bar 1) and T2 (grey bar 3) at Lag 2 and for the common component T1&2 (grey bar 2) at Lag 1 in Fig. 7									
$T_1M_1T_2M_2$	T_1	342.13 ± 28.14	2.03 ± 1.35	M_1	448.73 ± 32.69	0.12 ± 0.98	T_2	522.59 ± 22.07	1.67 ± 1.08
$T_1T_2M_1M_2$		404.95 ± 63.98	2.19 ± 1.27		404.95 ± 63.98	2.19 ± 1.27			
T_1_T_2M_1	T_1	376.40 ± 35.97	2.20 ± 1.27	_	452.16 ± 31.06	0.38 ± 1.44	T_2	521.45 ± 42.32	1.83 ± 1.43
$M_1M_2M_3M_4$	M_1	348.22 ± 31.18	0.95 ± 0.57	M_2	420.94 ± 49.94	1.38 ± 1.01	M_3	522.59 ± 29.01	1.18 ± 0.78

Values are mean ± SD of the components per cluster as described in the text. CS, cortical response to stream member; S_{1-3}, position of stimulus in RSVP stream: S_1 is always T_1 but S_2 can be blank, T_2 or M_2 and S_3 can be T_2 or M_1, depending on the stream. Units: time is in ms and is the peak latency from time 0 as defined in Fig. 1; peak amplitude is in Am x 10^{-8} (cf. Figs. 5-7). *Note that these values for T_1 and T_2 are the same.

cortical sources will be captured to some extent by the same electrode and, hence, the resulting P300 will be a (weighted) mix of the P300s in these different locations. This, in turn, might result in a broader distribution of the P300 as different cortical areas might show a slightly different P300 timing which, in turn, would conceal latency differences at the electrode level.

Results

Behavioural results

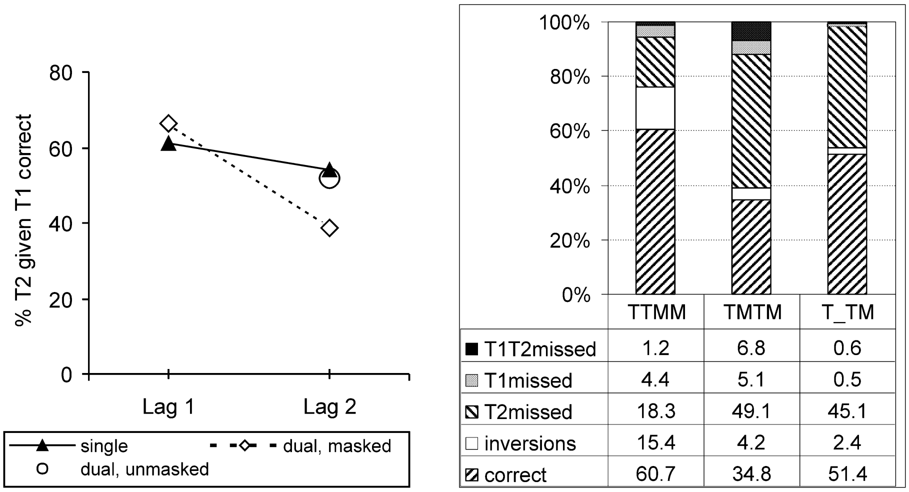
The results for the behavioural performance are shown in Fig. 3A. As expected, under dual-target instruction there was a reliable drop of performance at Lag 2 as compared to single-target performance: an AB effect. (Note that a full AB effect is also defined by a recovery of performance at ≈ Lag 5–6, which we did not investigate here. For the sake of clarity and simplicity we will nevertheless refer to the drop in performance at Lag 2 as an AB effect.) However, this drop was only obtained if T1 was masked ($t_9 = 4.951$, $P < 0.001$), but not if T1 was not masked ($t_9 = 0.284$, $P < 0.783$), corroborating the importance of a mask for the AB. We also saw Lag-1 sparing: performance was preserved at Lag 1, which produced a significant interaction of task (single vs. dual targets) and lag (Lag 1 vs. Lag 2): $F_9 = 50.158$, $P < 0.0001$. (Note that for single targets 'position' and not 'lag' is actually the appropriate term, as only one target was presented. The single targets occurred, however, at positions in the stream that were corresponding to the positions, i.e. lags, of the T2s in dual-target trials. We therefore use the term 'lag' for all conditions to enhance simplicity.) A more detailed analysis of the types of errors revealed a particularly pronounced rate of order confusions at Lag 1 (Fig. 3B). Even though the electrophysiological analysis of trials with these kinds of errors would have been of interest (an issue examined further in the Discussion) their small number and high interindividual variability prevented us from carrying it out. We thus further analysed only those trials in which the two targets were reported in the correct order. Panel B of Fig. 3 also reveals all types of behaviour that occurred for each dual target condition at each lag. It is important to point out that in the case of our study preserved performance on T2 at Lag 1 (i.e. Lag-1 sparing) did not go at the expense of T1: performance on T1 was at the same level for Lag 1 and 2 while performance on T2 dropped dramatically at Lag 2 if T1 was masked (i.e. AB).

Source localization

As described in Materials and methods and consistent with previous findings (Gross *et al*., 2004), we were able to identify three clusters of extrastriate sources that are believed to represent different components of an interactive attentional network: a prefrontal, a left TPF and a right TPF cluster (Fig. 4B–D). An additional occipital source cluster reflected the early processing of incoming visual stimuli (Fig. 4A), presumably operations of feature extraction (Blasdel & Salama, 1986).

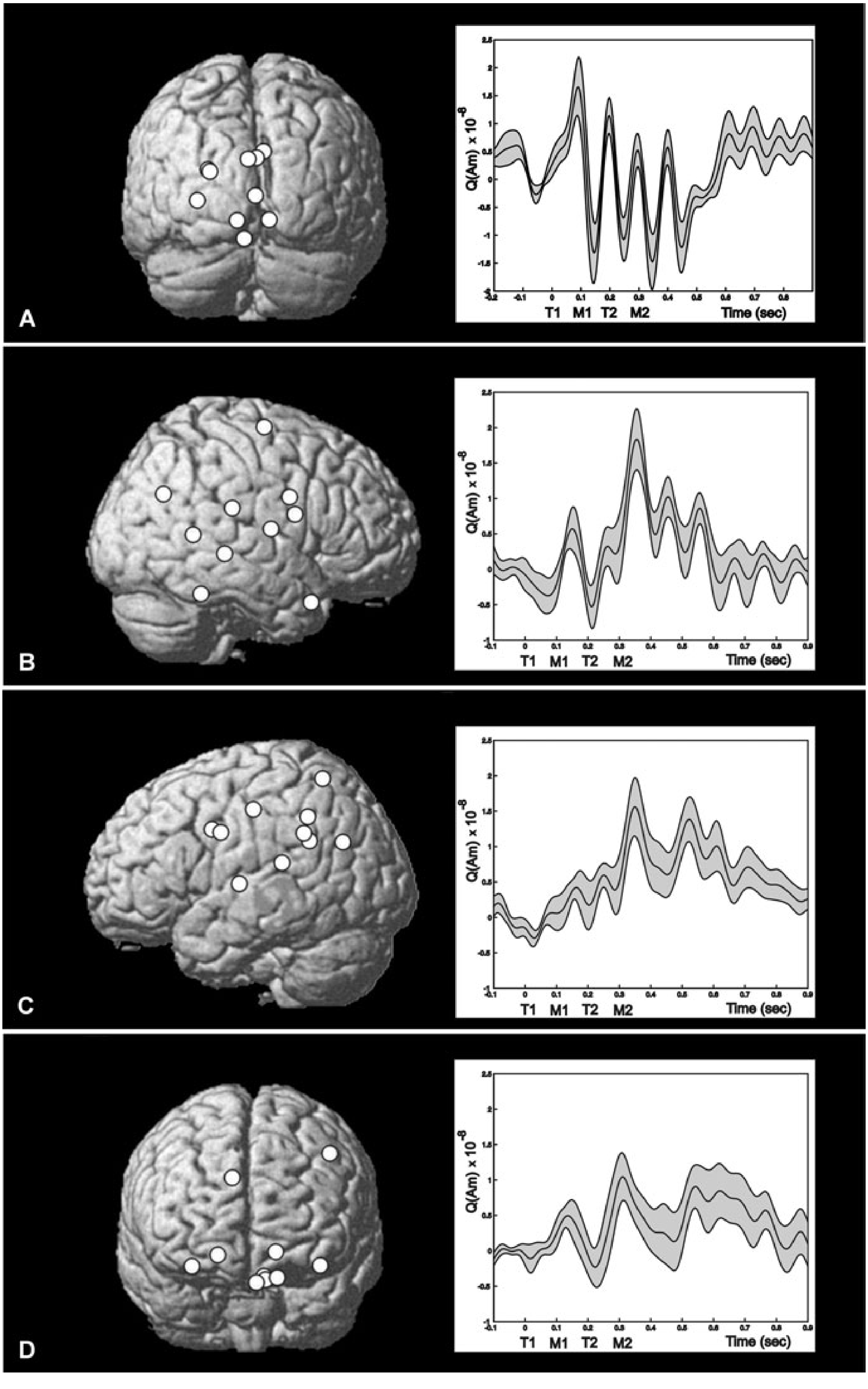
In eight out of 10 subjects we observed one occipital and two bilateral occipito-temporal sources (in two subjects only one occipito-temporal dipole could be fitted according to our standards), which is in agreement with previous findings (Tarkiainen *et al*., 2002). As occipital cortex has not been reported to be involved in the generation of the P300 ERP component, we did not analyse occipital signals any further. However, to give an impression of these signals we generated an occipital cluster based on the most medial occipital source in each individual. The averaged waveforms show regular biphasic responses every 100 ms that accurately reflect the SOA of the visual letter stream (on the right of Fig. 4A). However, responses to targets at the first stream position (i.e. T1 in all dual-target conditions) did not differ significantly from responses to masks at the same position ($Z = -1.376$, $P < 0.169$), supporting our decision not to further analyse occipital waveforms.

Although the two lateralized TPF clusters were anatomically more distributed they revealed high similarity of signals across individual sources within each of the two clusters (see SEM of waveforms in Fig. 4B and C; details are provided in Materials and methods). Therefore a functional match was the primary criterion for identifying a left and a right hemispheric cluster. The areas between frontal, temporal and parietal cortex have been shown to play a major role in the AB; e.g., patients with lesions in inferior frontal, superior temporal



	TTMM	TMTM	T_TM
■ T1T2missed	1.2	6.8	0.6
▨ T1missed	4.4	5.1	0.5
▧ T2missed	18.3	49.1	45.1
□ inversions	15.4	4.2	2.4
▨ correct	60.7	34.8	51.4

FIG. 3. Behavioural results. (A) The observed percentage of correct target reports: percentage of correct reports for the 'single target' condition and correct T2 performance given T1 correct for the 'dual target' conditions, respectively. 'Dual unmasked' refers to the T_TM condition where a target presented at the first position in the stream was followed by a gap of 150 ms (cf. Fig. 1) while a second target was presented immediately after the gap. 'Lag 1' indicates that T2 immediately followed T1 with an SOA of 100 ms. (B) The unconditionalized percentages for each behaviour type for the three dual-target conditions (TTMM, Lag 1; TMTM, Lag 2, T1 masked; T_TM, Lag 2, T1 unmasked): 'T1T2missed', both targets were missed; 'T1missed', T1 was missed yet T2 was reported; 'T2missed', T2 was missed yet T1 was reported; 'inversions', both targets were reported yet in reversed order; 'correct', both targets were reported in correct order.


A
Q(Am) x 10⁻⁸
T1 M1 T2 M2 Time (sec)
B
Q(Am) x 10⁻⁸
T1 M1 T2 M2 Time (sec)
C
Q(Am) x 10⁻⁸
T1 M1 T2 M2 Time (sec)
D
Q(Am) x 10⁻⁸
T1 M1 T2 M2 Time (sec)

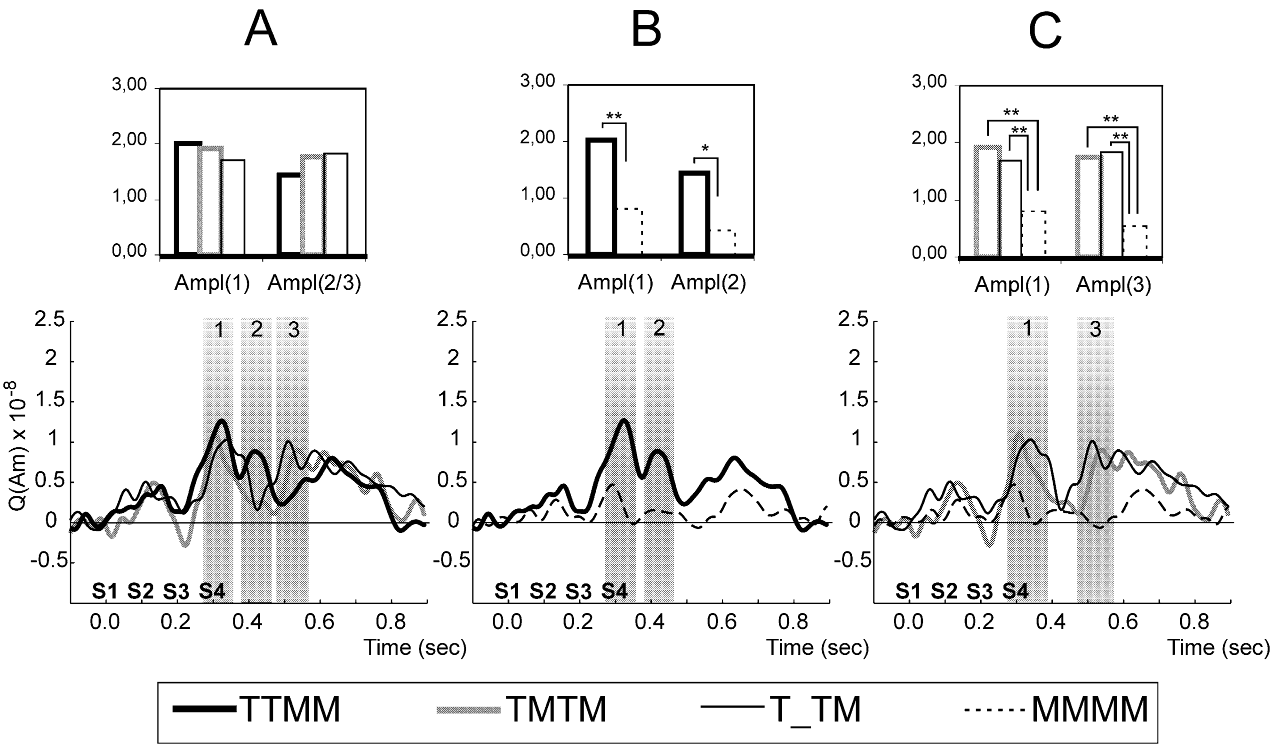


FIG. 5. Waveforms for the prefrontal (PFC) source cluster, time-locked to the first letter in the RSVP stream at 0 ms; S1–S4 indicate the onset of each letter. In the T_TM condition S2 was replaced by a gap. The thick black line represents the Lag-1 (dual target) condition, the thick grey line is the Lag-2 masked (dual target) condition, the thin black line is the Lag-2 unmasked (dual target) condition and, finally, the dotted line is the masks-only condition (shown merely as a baseline for target-related components). (A) Comparison of all three dual-target conditions; (B) comparison of the Lag-1 condition to the baseline (masks only); (C) similar baseline comparison for the Lag-2 dual-target conditions. The grey bars in each panel indicate relevant target-related components that are referred to in the text. The main target-related comparisons are included in a diagram at the top of each panel. The numbers on the *x*-axis denote to which grey bar the comparisons refer. Note that amplitudes in the diagrams are generally higher than in the corresponding waveforms. That is because amplitude comparisons were calculated on the basis of individual peaks disregarding individual latency variations. In the average waveforms these latency variations manifest themselves as a smearing-out of amplitude maxima and minima.

and inferior parietal areas show abnormal AB functions (Husain *et al.*, 1997; Shapiro *et al.*, 2002).

For each subject only one prefrontal source was fitted and included in the prefrontal cluster (Fig. 4D). Although there was some variation in the exact location across individuals there was quite a high similarity in the time course of the signals, as is suggested by the relatively low SEM across the trial interval (on the right of Fig. 4D). The individual sources in the prefrontal cortex (PFC) were distributed across anterior cingulate, dorsolateral, ventrolateral and orbital prefrontal locations (Fig. 4D). Each of these areas has been related to high-level attentional processing and working memory (Miller & Cohen, 2001). Anterior cingulate cortex has been shown to participate in target processing during the AB (Marois *et al.*, 2000) as well as in top-down control during letter decisions (Stephan *et al.*, 2003). The anterior cingulate cortex is thought to be involved in the detection and/or resolution of conflict signalled from other parts of the PFC, e.g. dorsolateral and ventrolateral parts (Botvinick *et al.*, 1999; Carter *et al.*, 2000). It has been proposed that ventrolateral and especially dorsolateral PFC, in turn, are involved in working memory consolidation and control (Goldman-Rakic, 1996; Glahn *et al.*, 2002; Mottaghy *et al.*, 2002), whereas orbitofrontal cortex is thought to be concerned with response selection and evaluation (Freedman *et al.*, 1998), yet there is evidence as well that orbital prefrontal cortex is directly involved in visual attention (Nobre *et al.*, 1999). In addition, activation patterns in the orbital prefrontal cortex might discriminate between frequent and infrequent 'blinkers' in AB tasks (Feinstein *et al.*, 2004).

M300 waveforms

Given the possibility that the two targets are integrated at Lag 1, we examined the data for a common T1- and T2-related M300 component in the three relevant clusters. Most relevant for this comparison are the waveforms from the Lag-1 condition (TTMM). As described in detail below, a comparison across Figs 5–7 reveals two distinct waveform components, for the two targets, in all but condition TTMM at left TPF, where either separate T1- and T2-related M300 responses are smeared into a common response or a single integrated process is reflected by the single component in this cluster.

FIG. 4. Locations of the sources in each cluster. Individually fitted dipoles were included into the four clusters shown in Panels A to D (10 dipoles per cluster, one per subject). (A) Sources in the occipital cluster that are excluded from further analysis. (B) Sources in the right TPF cluster, (C) in the left TPF cluster, (D) in the prefrontal cluster. Individual source locations were mapped onto a standard brain by using SPM99 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London). Grand averages, at the far right of each panel, illustrate mean source waveforms ± SEM for the dual target, masked condition (correct report of both targets) in each cluster. The clusters were determined by examining the anatomical overlap and most importantly the similarity of signal properties (by minimizing the SEM) across the subject's multidipole models (details in Materials and methods).

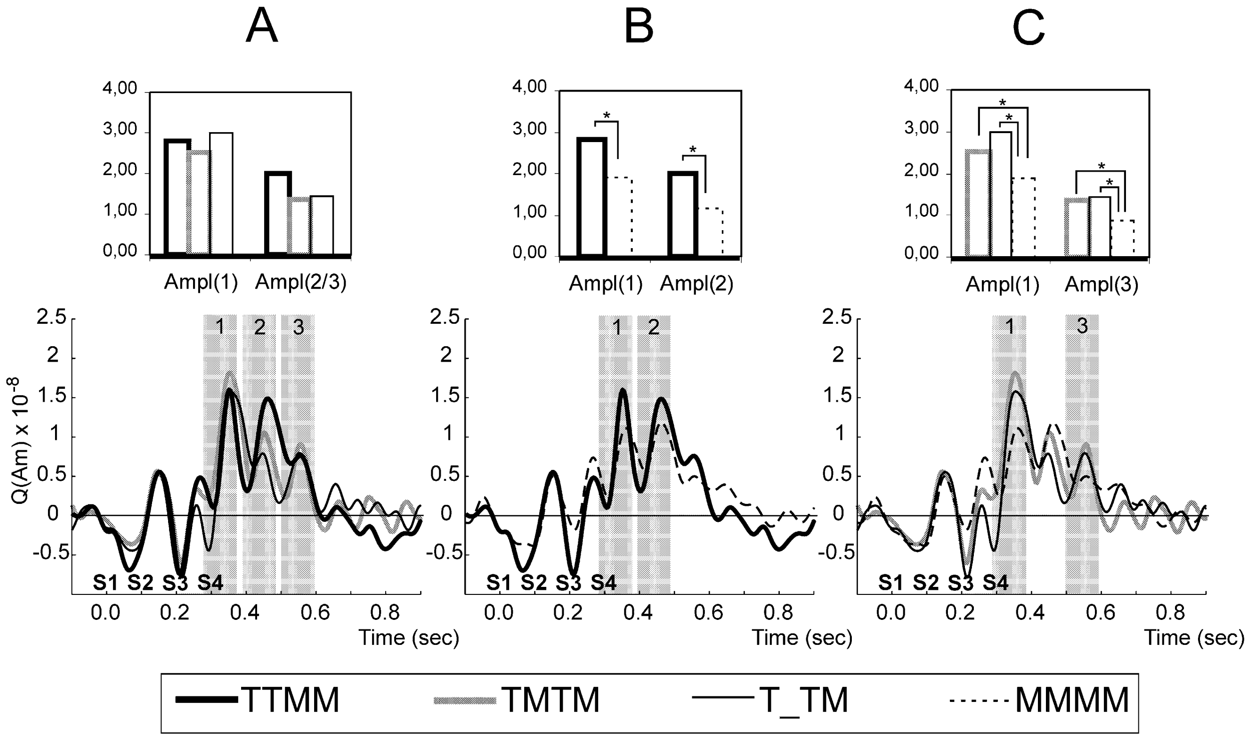


FIG. 6. Waveforms for the right TPF source cluster, time-locked to the first letter in the RSVP stream at 0 ms; S1–S4 indicate the onset of each letter. In the T_TM condition S2 was replaced by a gap. The thick black line represents the Lag-1 (dual target) condition, the thick grey line is the Lag-2 masked (dual target) condition, the thin black line is the Lag-2 unmasked (dual target) condition and, finally, the dotted line is the masks-only condition (shown merely as a baseline for target-related components). (A) Comparison of all three dual-target conditions; (B) comparison of the Lag-1 condition to the baseline (masks only); (C) similar baseline comparison for the Lag-2 dual-target conditions. The grey bars in each panel indicate relevant target-related components that are referred to in the text. The main target-related comparisons are included in a diagram at the top of each panel. The numbers on the *x*-axis denote to which grey bar the comparisons refer. Note that amplitudes in the diagrams are generally higher than in the corresponding waveforms. That is because amplitude comparisons were calculated on the basis of individual peaks disregarding individual latency variations. In the average waveforms these latency variations manifest themselves as a smearing-out of amplitude maxima and minima.

For PFC, clearly there are two distinct components for T1 and T2 (Fig. 5B: T1-related, grey bar 1; T2-related, grey bar 2). Note that the early competition model (Potter *et al.*, 2002; in press) predicts that at very short SOAs T2 is often identified prior to T1. Hence, one might be inclined to assume that the first M300 peak at Lag 1 might in fact be related to T2. We thank Roberto Dell'Acqua for pointing this out to us. However, advantages for T2 in identification speed were only reported for SOAs ≈ 50 ms (Potter *et al.* in press), hence much shorter than the 100 ms SOA employed here. In addition, our behavioural data do not provide any evidence for a trade-off for T1 performance in favour of T2 with our paradigm. Finally, the first M300 peak in the Lag 1 condition is almost identical in shape and latency to the Lag 2 conditions, in which case it can be taken for granted that this peak reflects T1-related processes.

Both target components are significantly different from the masks only condition (for T1, $Z = -2.701$, $P < 0.007$; for T2, $Z = -2.090$, $P < 0.037$), while showing no difference in amplitude to the target-related M300 components (Fig. 5A) from both Lag-2 target conditions (all $Z > -0.968$; $P > 0.333$). These M300 responses in the Lag-2 conditions arising from T1 and T2, respectively (T1-related, grey bar 1; T2-related, grey bar 3 in Fig. 5C) are in turn significantly different from the masks only condition (all $Z < -2.599$; $P < 0.009$).

A very similar pattern is obtained for right TPF (Fig. 6A–C). All conditions show a regular series of responses that mirror the incoming visual information, with the masks only condition (MMMM) showing this rhythm in its purest form. On top of this pattern we see the target conditions, which clearly differ from the mask condition (see Fig. 6B and C). Again, we see two distinct target-related M300 components for the Lag-1 condition (grey bars 1 and 2 in Fig. 6B), as are similarly revealed in the Lag-2 dual-target conditions (Fig. 6C). Both components (Fig. 6B) differ significantly from the masks only condition (for T1, $Z = -2.191$, $P < 0.028$; for T2, $Z = -2.090$, $P < 0.037$). In both Lag-2 conditions distinct target-related M300 components for T1 and T2 are also observed (T1-related, grey bar 1; T2-related, grey bar 3 in Fig. 6C), which differ significantly from the masks only condition (all $Z < -2.293$; $P < 0.022$). Comparing the three dual-target conditions (Fig. 6A) we see no significant amplitude differences for target-related M300 components.

The results are very different for the left TPF source cluster (see Fig. 7A–C). In contrast to right TPF and PFC, only one distinct target-related M300 component is obtained for the Lag-1 condition, as indicated by the grey bar 2 in Fig. 7B (TTMM vs. MMMM, $Z = -2.191$, $P < 0.028$). It could be, however, that jitter across participants may smear individually distinct target-related peaks and allow a single component to emerge at the group level. Figure 8 suggests that this does not seem to be the case. The SEM of the waveforms (Fig. 8A and B) indicates that the variability across the group at Lag 1 (Fig. 8A) was not higher than the variability at Lag 2 (Fig. 8B). In addition, Fig. 8C shows the example of a single participant with two clearly separated components at Lag 2 and with a single component at Lag 1. Therefore, we interpret the group waveform in the left TPF at Lag 1 as reflecting a single M300 component which is not simply a result of more variability across participants. We cannot exclude,

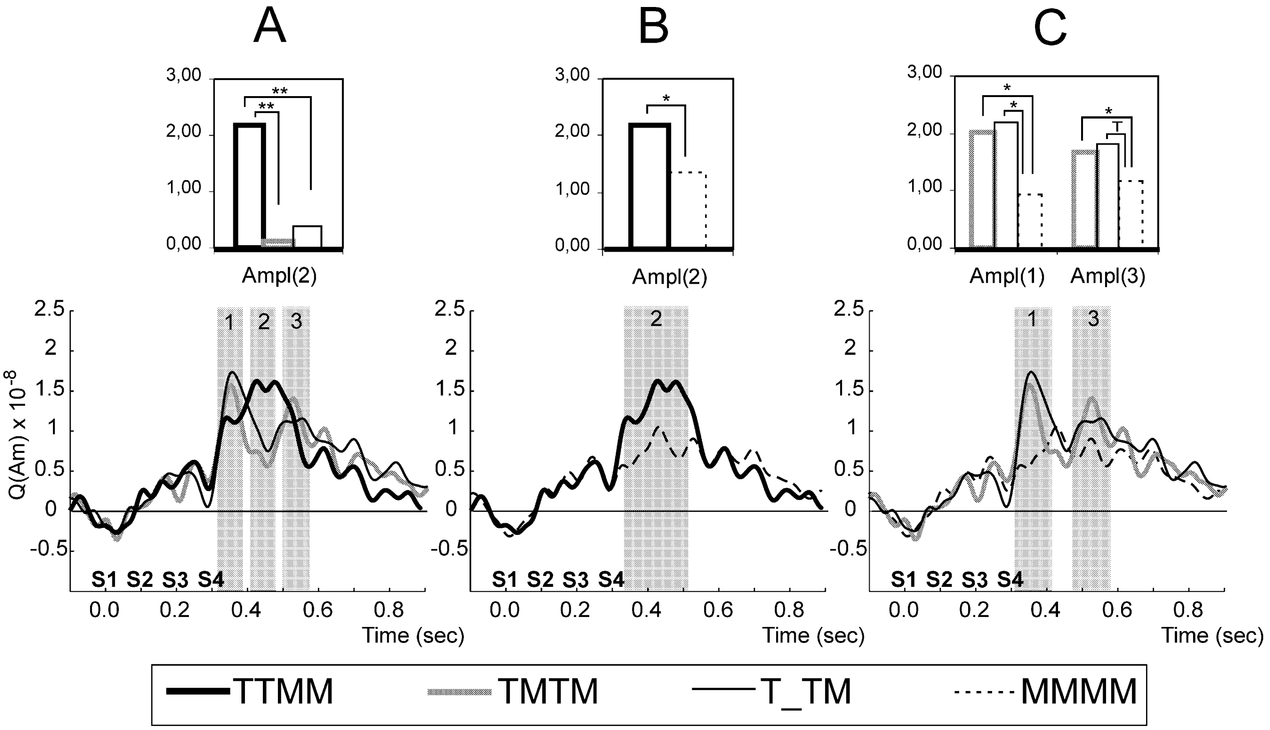


FIG. 7. Waveforms for the left TPF source cluster, time-locked to the first letter in the RSVP stream at 0 ms; S1–S4 indicate the onset of each letter. In the T_TM condition S2 was replaced by a gap. The thick black line represents the Lag-1 (dual target) condition, the thick grey line is the Lag-2 masked (dual target) condition, the thin black line is the Lag-2 unmasked (dual target) condition and, finally, the dotted line is the masks-only condition (shown merely as a baseline for target-related components). (A) Comparison of all three dual-target conditions; (B) comparison of the Lag-1 condition to the baseline (masks only); (C) similar baseline comparison for the Lag-2 dual-target conditions. The grey bars in each panel indicate relevant target-related components that are referred to in the text. The main target-related comparisons are included in a diagram at the top of each panel. The numbers on the *x*-axis denote to which grey bar the comparisons refer. Note that amplitudes in the diagrams are generally higher than in the corresponding waveforms. That is because amplitude comparisons were calculated on the basis of individual peaks disregarding individual latency variations. In the average waveforms these latency variations manifest themselves as a smearing-out of amplitude maxima and minima.

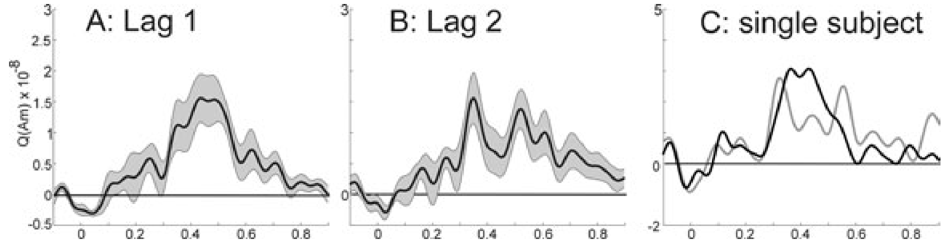


FIG. 8. Variability of the waveforms in left TPF. (A) Group average at Lag 1 along with the SEM; (B) SEM and average for the Lag 2, masked condition; (C) waveforms for Lag 1 (black) and Lag 2, masked (grey) in a single subject. Further explanations in the text.

however, the possibility that intraindividual variations at the trial level may lead to a smearing of two separate target-related processes (to T1 and T2, respectively). However, smearing across trials leaves the question unresolved of why this seems to be special in left TPF, at Lag 1. Taken altogether this pattern can either be interpreted as a single component that reflects a single process in left TPF related to both targets, or as a single component that reflects two distinct processes that are smeared at the trial level. In either case this points to a special functional role of left TPF and alternative interpretations will be provided in the Discussion.

In contrast to Lag 1, the Lag-2 conditions show two distinct target-related M300 components for T1 and T2 (T1-related, grey bar 1; T2-related, grey bar 3 in Fig. 7C) that differ significantly from the distractor condition, apart from the T2-related component in the T_TM condition, which was marginally significant (for T1: TMTM vs. MMMM, $Z = -2.191$, $P < 0.028$; T_TM vs. MMMM, $Z = -2.803$, $P < 0.005$; for T2: TMTM vs. MMMM, $Z = -2.090$, $P < 0.037$; T_TM vs. MMMM, $Z = -1.886$; $P < 0.059$). Comparing the three dual-target conditions (Fig. 7A) we see a significant amplitude difference ($Z = -2.090$, $P < 0.037$) for T2-related M300 components between Lag 1 (TTMM, stronger) and masked Lag 2 (TMTM, weaker).

M300 latency

Given the possibility that the two targets compete for access to attentional resources at Lag 1, we also looked for differences in latencies of T1- and T2-related M300 components across the three relevant clusters.

In PFC, the latency of the T1-related component in the Lag-1 condition did not differ significantly from the T1-related components in either Lag-2 condition (grey bar 1 in Fig. 5A: TTMM vs. TMTM, $t_9 = 0.896$, $P < 0.394$; TTMM vs. T_TM, $t_9 = 1.607$, $P < 0.143$). However, somewhat counter-intuitively, among the Lag-2 conditions T1 was processed faster if it was followed by a mask than if no mask letter intervened between T1 and T2 (TMTM vs. T_TM, $t_9 = 2.259$, $P < 0.05$).

Somewhat trivially, the T2-related M300 component for the Lag-1 condition reached its peak significantly earlier than in the Lag-2 condition (grey bar 2 vs. 3 in Fig. 5A; TTMM vs. TMTM, $t_9 = 9.226$, $P < 0.0001$; TTMM vs. T_TM, $t_9 = 6.550$; $P < 0.0001$). However, the mean peak latency difference between Lag-1 and Lag-2 conditions (averaged) corresponded exactly to the 100-ms difference in lag or SOA (cf. Table 2), suggesting that the component was not delayed at Lag 1. Finally, the T2-related M300 component in the T_TM condition reached its peak significantly earlier than in the TMTM condition: $t_9 = 3.051$, $P < 0.014$, which reverses the pattern observed for T1. Taken together these results suggest that without an intervening mask (T_TM or TTMM) the two targets can be processed in very close temporal succession.

No significant latency differences could be observed for the right TPF cluster apart from the earlier T2-related peak in the Lag-1 condition as compared to the Lag-2 condition (grey bar 2 vs. 3 in Fig. 6A). Again, this effect was solely due to the difference in SOA between Lag 1 and Lag 2. However, the T1-related M300 responses revealed a statistical tendency to peak earlier in the Lag-1 condition (TTMM) than in either Lag-2 condition (T_TM, $t_9 = 1.991$, $P < 0.078$; TMTM, $t_9 = 2.237$, $P < 0.052$).

In left TPF, the combined T1–T2-related component at Lag 1 peaked significantly later than the T1-related M300 component ($t_9 = 2.784$, $P < 0.021$) but significantly earlier than the T2-related M300 component ($t_9 = 4.887$; $P < 0.001$) in the TMTM condition (Fig. 7A). Similar latency differences can be observed in comparison to the T_TM condition as well, yet the delay with respect to the T1-related M300 component was only numerically present [T1–T2 (TTMM) vs. T1 (T_TM): $t_9 = 1.214$, $P < 0.256$; T1–T2 (TTMM) vs. T2 (T_TM): $t_9 = 4.897$, $P < 0.001$]. The lack of a significant difference between the T1–T2- and T1-related M300 components is due to the fact that the T1-related response in the T_TM condition was significantly delayed with respect to the TMTM condition as well ($t_9 = 2.717$, $P < 0.024$).

Discussion

The primary purpose of the present study was to gain insight into the neural processes underlying the 'Lag-1 sparing' phenomenon. One of the two hypotheses we investigated is whether presenting two targets in very close temporal succession induces competition between them (Potter *et al*., 2002; Hommel & Akyürek, in press; Potter *et al*., in press). If so, one might expect that especially T1-related M300 components would be delayed for Lag 1. We found some evidence for a delay in left TPF, where the T1 component ('embedded' into the single M300 peak) occurred later in the Lag-1 condition (TTMM) than in the other conditions. This delay in T1 processing was accompanied by an earlier peak for T2 as there was only a single M300 response. This could point to a certain amount of competition if one takes into consideration that on some trials T2 might have been processed prior to T1. In fact such a processing advantage for T2 has been recently demonstrated by Potter *et al*. (2005) by means of semantic priming. At very short SOAs (< 100 ms) T2 primes T1, suggesting that on a significant number of trials T2 is processed prior to T1. Although Potter *et al*. (2005) did not observe this effect at the SOA employed here (100 ms) T2 might still be processed prior to T1 in the subnetwork most probably related to identification (but not consolidation) on some trials. The left TPF might be a possible candidate for such a subnetwork and the single M300 response in this cluster might reflect a mixture (smearing) at the intrasubject level of trials where T1 was processed first and of trials where T1 was processed second. It is, however, important to point out that we did not find any behavioural evidence for performance on T1 being traded for performance on T2 (Fig. 2B), nor did we find similar smearing in other brain areas.

In contrast, in right TPF a tendency was revealed for T1 to be processed even faster at Lag 1. The results with respect to amplitudes do not support competition either: weaker amplitudes at Lag 1 that would point to competition were not observed, yet the common T1–T2-related response in left TPF was significantly stronger than the T2-related component at Lag 2. Thus we obtained little evidence for competition, suggesting that this factor did not play a major role in producing the present outcome. This is not to say that the two targets do not compete at all: note that we only analysed trials in which both targets were reported correctly, which may mean that we excluded all trials in which competition was strong enough to suppress one of the targets. If so, one would expect more systematic latency delays and amplitude differences in trials where one target was missed which, in the present study, were too infrequent to allow a meaningful analysis. In any case, however, we can conclude that competition between the two targets is unlikely to take place in all or a majority of the trials, suggesting that an account of Lag-1 sparing exclusively in terms of competition cannot completely explain our data.

The second hypothesis we considered is that two temporally close targets may become integrated into a single episode (Shapiro *et al*., 1994; Chun & Potter, 1995). If so, we would have expected a single working memory update, i.e. a single M300 response, related to the two targets at Lag 1. On the one hand it seems clear that this does not occur across the whole attentional network, as no evidence was observed in PFC and right TPF. We take this to mean that the system does not treat the two targets as one event in these brain areas. On the other hand, we observed a waveform resembling a single M300 in left TPF: either the two target-related responses are smeared because the T1-related component occurs later while the T2-related component occurs earlier, or the T1 and T2 signals are merged into a single representation in this area. Before discussing the possible functional implications of this observation let us first briefly consider the roles the three analysed cortical clusters are likely to play in the AB.

PFC has been strongly associated with WM and, indeed, all the prefrontal sources we identified (see Fig. 4) have been related to high-level attentional processing and WM (Miller & Cohen, 2001). This assumed central role of PFC for attentional selection and WM consolidation and maintenance is consistent with the finding that the activation patterns in the PFC cluster are most directly correlated with behavioural performance in an AB task (Kessler *et al*., 2005). The reported PFC waveforms reveal fast processing of T1 and delayed processing of T2 in masked Lag-2 trials compared to unmasked Lag-2 trials. Hence, without an intervening mask the two targets can be processed in close temporal proximity at Lag 1 and Lag 2. These findings suggest that an important factor in the explanation of Lag-1 sparing could be the lack of an intervening mask, which obviously impedes the transition from T1 to T2 processing at Lag 2 (Raymond *et al*., 1992; Di Lollo *et al*., 2005; Kessler *et al*., 2005). Therefore, unimpeded target processing seems more important than integration of the two targets into a single event representation with respect to successful working memory consolidation in PFC.

On the basis of empirical evidence we take as our working hypothesis that the cortical areas captured by our right TPF cluster are involved in mediating PFC and left TPF (Husain *et al.*, 1997; Shapiro *et al.*, 2002) and in the binding of temporal order to identity (Harrington & Haaland, 1999), whereas areas in our left TPF cluster are likely to be responsible for letter matching and recognition processes (Petersen & Fiez, 1993; Stephan *et al.*, 2003). In this hypothetical division of labour, the absence of any evidence of smearing in the PFC cluster suggests that, in fully successful trials, WM is updated twice, once for each target, and for both lags. Thus, with regard to WM proper, our findings do not suggest that successive target stimuli are merged into a single neural code. If we assume that the successful binding of the identity and temporal position (i.e. order) of a target depends on the temporal contrast between target-related signals in the right TPF region it is logical to conclude that successful performance on both targets in terms of identity and order is accompanied by distinct components in this region (right TPF).

In contrast to the other two clusters, the left TPF cluster seems to show only a single M300 component. As described in Results, we interpret the waveform pattern at Lag 1 as a single component as the interindividual variability was not enhanced in the Lag 1 condition. However, the question remains whether trial-by-trial intraindividual variability might have smeared two distinct target-related processes into one M300 component: a single component does not necessarily reflect a single target-related process. Accordingly, this pattern might suggest that the cortical areas captured by this cluster can process the two targets almost in parallel, as both targets are reported. This hypothesis is supported by the results of flanker tasks, in which a spatially defined target is surrounded by to-be-ignored, response-compatible or -incompatible nontargets (Eriksen & Eriksen, 1974). The nontargets cannot be fully ignored if they appear together with the target and still affect performance if they appear somewhat (50–100 ms) later (Eriksen & Schultz, 1979). This points to the existence of temporal matching and recognition windows that are not strictly bound to the time of onset or the number of stimuli and which, according to our data, are more confined to left TPF areas.

The proposed dissociation between matching and recognition in left TPF and order-identity integration in right TPF also dovetails nicely with a recent paper (Giesbrecht & Kingstone, 2004) where a split-brain patient showed a stronger AB if T2s were displayed to the right hemisphere. According to our data it seems more crucial for correct performance on both targets that right TPF shows more clearly separated target responses than left TPF. As pointed out, effective order-identity integration would have to be strictly sequential whereas during matching and recognition a temporal overlap of specialized processes may be tolerable.

Specifically, with regard to the present study we contend that both targets occurring during such a temporal matching and recognition window are processed simultaneously, apparently up to identification, at least in the case of stimuli that are as simple and as overlearned as those used in this study. In fact, the simplicity of the target set (only two letters) might have allowed for the generation of a target template that comprised both letters. If this was the case then two subsequent targets, as happens to be the case at Lag 1, could be simultaneously matched to such a 'combined' template and, hence, require only a single matching process in left TPF, reflected by the single M300 component. On the one hand this would explain enhanced performance at Lag 1 in studies that employed very simple target sets such as the one used here. On the other hand, it would be more difficult to generate 'combined' templates in studies that use larger target sets (e.g. up to nine digits), hence leading to poorer performance as observed by Hommel and Akyürek (2005).

To put this another way, assume there is an advantage to a single matching process in overcoming AB-like deficits, in much the same way as there is an advantage to processing two attributes of a single target, relative to processing the same two attributes, one on each of two targets (Duncan, 1984). Thus the Lag-1 condition confers an advantage on identity processing in the left TPF region as the two targets are matched as a single unit. However, the judgement of the temporal order of the two targets is poor, as right TPF and PFC must reconcile two M300 waveforms with the single waveform output of left TPF. This reconciliation process leads to the temporal order deficits corroborated by behavioural data showing order confusions at Lag 1 (cf. Fig. 3B; also Hommel & Akyürek, 2005).

However, it is important to point out that the interpretation of our findings has be generalized with care to a comprehensive explanation of the Lag-1 sparing phenomenon. In several studies (Potter *et al.*, 2002; Hommel & Akyürek, 2005) a clear trade-off for T1 performance in favour of T2 was observed that was not replicated here due to the simplicity of the paradigm. Apart from the size of the target set and the complexity of the task-set switch between T1 and T2 (Visser *et al.*, 1999), the complexity of identification for each target might also affect processing at Lag 1. That is, Potter *et al.* (2005) have employed 4- or 5-letter words as targets. Obviously, these stimuli necessitate a more complex identification than single letters; hence, T1 identification might be more susceptible to interference by T2. This may result in a higher probability for T2 being processed prior to and more accurately than T1 at (very) short lags (Potter *et al.*, 2002, 2005). So what may the results in the simple paradigm employed here reveal about the processes at Lag 1 in general? One way of looking at it would be to assume that the different paradigms differ in the frequency distribution of occurrence for each potential process that is possible at Lag 1: words might enhance competition during identification, large set sizes might increase the trade-off for T1 performance in favour of T2 in general, task switches might enhance the complexity of reconfiguration (transition from T1 to T2), while simple target configurations (one stream, two letters) would allow for a majority of 'true' sparing trials to occur. Hence, the paradigm employed here allowed investigation of the conditions under which performance is truly spared and pointed to matching and recognition networks (left TPF) as a potential candidate where processes may overlap or may be integrated in a way that allows for most efficient processing and spared performance.

In summary, the present study analysed the M300 waveform components, generated by the presence of two targets in an attentional blink task, in an attempt to explain the frequently observed Lag-1 sparing phenomenon. The results we obtained lend support to the notion that, at the level of consolidation and integration, i.e. prefrontal and right TPF cortex, the human brain is able to disentangle the signals from the two targets, treating them as separate events. The lack of an intervening mask at Lag 1 thus seems to allow proximate yet distinct consolidation of the two targets. Processing is different in matching and recognition networks, i.e. left TPF cortex, where the signals arising from the two targets are either smeared or processed in a single step. As little behavioural evidence was observed for early competition between the two targets we propose that the two subsequent targets might be matched in a common process to a 'combined' template, leading to enhanced performance in the behaviourally unique Lag-1 sparing condition.

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Abbreviations

AB, attentional blink; MEG, magnetoencephalography; PFC, prefrontal cortex; RSVP, rapid serial visual presentation; SOA, stimulus onset asynchrony; T1, first target in an AB task; T2, second target in an AB task; TPF, temporo-parieto-frontal cortex; WM, working memory.

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