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RESEARCH****Research Report****ERPs predict the appearance of visual stimuli in a temporal selection task****Michael Niedeggen^{a,*}, Guido Hesselmann^a, Arash Sahraie^b, Maarten Milders^b**^aInstitute of Experimental Psychology II, Heinrich-Heine-University, D-40225 Düsseldorf, Germany^bVision Research Laboratories, School of Psychology, University of Aberdeen, Aberdeen, UK

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ABSTRACT

In contrast to the visual spatial domain, the effect of attention on sensory processing and stimulus appearance in temporal selection tasks is still controversial. Using a rapid serial visual presentation (RSVP) procedure, we examined whether the stimulus onset asynchrony (SOA) between a color cue and a motion target affects the appearance of the latter. Event-related brain potentials (ERPs) recorded simultaneously allowed us to test whether a change in the targets' appearance is associated with a modulation of the sensory ERP components. In the experimental condition 'SOA', the temporal interval between the cue and the target was varied between 0 and 300 ms. In a control condition, the physical appearance of the motion target was varied (level of coherence: 25–100%) while holding the cue–target SOA constant (300 ms). In trials when the participant detected the target motion, his/her task was to report the strength of the perceived motion on a 5-point scale. In both conditions, the mean rating of the target's appearance increased monotonically with increasing SOA and the level of coherence, respectively. The psychophysical ratings were associated with an increase of a negative deflection about 200 ms (N200) related to the sensory processing of visual motion. The physical variation of motion coherence and the variation of the cue–target SOA affected the N200 response in similar fashion. These results indicate that sensory processing is also modulated by attentional resources in temporal selection tasks which – in turn – affect the appearance of the relevant target stimulus.

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1. Introduction

The effect of attentional deployment in visual spatial tasks has been examined in numerous physiological and psychophysical studies. Converging evidence from single-unit recordings (Chelazzi et al., 1993), ERP recordings (Luck, 1995), and functional brain imaging (Corbetta and Shulman, 1998) indicate that attention modulates early visual information processing. Correspondingly, a deployment of attention was found to modify the appearance of visual features, such as the perceived contrast (Carrasco et al., 2004).

However, it is questionable whether this effects can be transferred to tasks requiring temporal instead of spatial selection. In order to test the temporal limits of attention, the rapid serial visual presentation (RSVP) technique (Broadbent and Broadbent, 1987) has been established (Fig. 1). Subjects are instructed to detect two (or more) targets embedded in a rapid series of irrelevant visual events presented at a rate of approximately 10 Hz. In an RSVP trial, the identification or detection of the second target (T2) is significantly impaired for approximately 500 ms following the presentation – and detection – of the first target (T1). This reliable effect has

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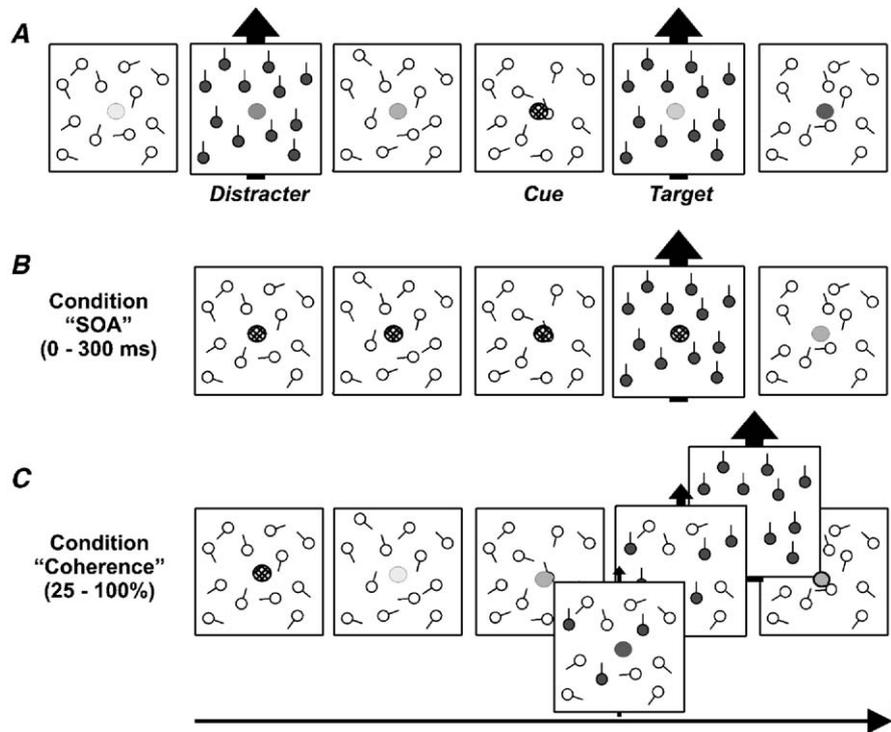


Fig. 1 – A schematic diagram of the stimulus configuration in a rapid serial visual presentation (RSVP) trial, and the experimental conditions (A) Continuously moving dots were presented in the “global” RSVP stream. Open circles indicate dots following a random walk, closed circles indicate dots moving coherently on a predefined direction (upwards) for 100 ms. The “local” RSVP stream was defined by a fixation point changing its color occasionally for 100 ms (for reasons of illustration: different levels of grey). In each trial, the onset of a red fixation point (here: hatched) was the cue signaling the target defined by the onset of an epoch of coherent motion. Episodes of coherent motion prior to the cue (distracters) had to be ignored. Following each trial, the perceived strength of the coherent target motion had to be indicated on a 5-point scale. (B) In the experimental condition ‘SOA’, the temporal interval between the onset of the color cue and the motion target was varied between 0 and 300 ms (indicated by the different positions of the hatched fixation point within the RSVP sequence). (C) The experimental condition ‘coherence’ provided a reference function. Here, the percentage of correlated moving dots defining the target motion was varied (25–100%) at a constant SOA of 300 ms.

been labeled as ‘attentional blink’ (Shapiro et al., 1994), and its determinants have been examined in numerous studies (for reviews, see Shapiro, 2001).

Following the findings in visual–spatial attention tasks, the deficit in T2 detection or identification is predicted to be correlated with a transient suppression in sensory processing. This view was supported by Valdes-Sosa et al. (1998, 2000) using an RSVP sequence defined by visual motion stimuli. Two superimposed sets of dynamic dots defined a transparent motion and subjects had to detect two short epochs of linear motion (T1 and T2) in one of the two surfaces. If the inter-target interval was short (< 500 ms), and if a switch between the surfaces was required, detection of T2 was significantly impaired. More importantly, the deficit in detection was correlated with a significant reduction of the sensory ERP components (Pinilla et al., 2001). The authors concluded that this type of object-based attention operates at an early level of perception, and that the reduction in sensory ERPs is related to the competition of rival motion signals.

However, ERP studies based on the serial presentation of single letters or words (Vogel et al., 1998; Rolke et al., 2001) revealed that the impairment in T2 detection is not correlated

with an attenuation of visually evoked responses. These findings are congruent with the idea that the phenomenon is not attributed to a suppression of T2 at sensory level but to a competition or interference at a higher level of the visual short-term memory (Chun and Potter, 1995).

We developed a RSVP task which requires the detection of coherent visual motion and shares some characteristics with the paradigm developed by Valdes-Sosa et al. (1998, 2000). A ‘local’ RSVP stream was defined by frequent changes in color of a fixation point. In an annulus centered on the fixation point, an array of dynamic dots served as the ‘global’ RSVP stream. The subject had to attend to the fixation point, awaiting the onset of a unique occurrence of a red fixation point which acted as a cue to switch attention to the ‘motion’ RSVP stream where a brief episode of coherent motion (the ‘target’) had to be detected (for a similar experimental setup, see Joseph et al., 1997). A series of psychophysical experiments showed that the detectability of the target deteriorated if the temporal delay between cue and target was below 300 ms (Sahraie et al., 2001). In contrast to Valdes-Sosa et al. (1998, 2000), the deficit in the detection of a target motion was not induced by the necessity to switch between surfaces but

critically depended on the presence of short epochs of coherent motion preceding the cue (distracters). We recently proposed that these distracters gradually activate a frontally located suppression mechanism preventing a higher order processing of simple motion stimuli (Niedeggen et al., 2004).

With respect to the visually evoked responses to the onset of a target motion our findings were ambiguous (Niedeggen et al., 2002). The onset of the target stimulus evoked the motion-sensitive N200, a posterior negativity peaking at about 200 ms (Bach and Ullrich, 1994; Kubová et al., 1995; Niedeggen and Wist, 1999). If we focused our analysis on the difference between correctly detected and missed targets at a given cue–target SOA (0 ms), no effect on the N200 amplitude or latency was found. This finding was in line with the ‘late selection’ account in temporal selection (Vogel et al., 1998) and supported the notion that the transient deficit in motion processing could not be due to an attenuation of sensory processing. However, if we focused on the correctly detected trials and analyzed the effect of the increasing cue–target SOA (0–300 ms), a significant increase of the N200 amplitude was found. Such a modulation parallels the findings of Pinilla et al. (2001) indicating that sensory processing is modulated in temporal selection tasks.

The finding that the N200 amplitude in detected targets varies as a function of the cue–target SOA leads itself to the question whether the ERP effect is associated with a change in the appearance of the target motion. A previous ERP study has shown that a reduction in the N200 can be obtained by reducing the perceived speed of a target motion (Muller et al., 2004). However, we assumed that the amplitude reduction obtained in our RSVP task is rather associated with the perceived strength of the global motion signal. Such a relationship has already been established in ERP (Niedeggen and Wist, 1999) and MEG (Nakamura et al., 2003) studies, and its hemodynamic correlate has been localized using brain imaging in the motion-sensitive region V5 in the visual cortex (Heeger et al., 2000; Rees et al., 2000). More importantly, in our previous RSVP studies, subjects reported that the appearance of the detected target motion varied from trial to trial: the global coherent target motion (defined by 100% coherently moving dots) was perceived as ‘weaker’ – though not slower – if the temporal distance to the onset of the color cue decreased.

In the current study, we therefore introduced a rating procedure to test whether the appearance of a detected target motion – defined in terms of the strength of the global motion signal – systematically depends on the stimulus onset asynchrony (condition ‘SOA’) between the cue and the target. Moreover, we examined whether the motion-evoked N200 is also related to the appearance of a visual motion stimulus if its strength is physically constant but varied as a function of the cue–target interval. In order to provide a reference function, we also introduced the condition ‘coherence’. Here, the cue–target SOA was held constant at 300 ms with the target’s coherence varying between 25% and 100% correlated moving dots (see Fig. 1).

With respect to our previous results (Niedeggen et al., 2002), we hypothesized that a decrease of the cue–target SOA will reduce the sensory response to the target motion. Following the psychophysical findings in visuospatial tasks (Carrasco et al.,

2004), we expected the physiological effect to be correlated with a modulation of the strength of the motion signal perceived.

2. Results

2.1. Psychophysics

We tested whether the appearance of a coherent global motion (100% correlated moving dots, direction upwards) can be modified if the temporal distance between the cue and the target is varied (condition ‘SOA’). In the same experimental session, trials were randomly interleaved in which a target at constant SOA (300 ms) but varying signal strength (condition ‘Coherence’) was presented.

The results of the psychophysical procedure are shown in Table 1. In the condition ‘Coherence’, we obtained a rating function which clearly depended on the signal strength defined by the percentage of correlated moving pixels. At a maximum percentage of coherence (100% correlated moving dots), mean rating was 3.03 (SEM = 0.09) on the 5-point rating scale (range: 0–4). With decreasing percentage of correlated motion signals, the subjects’ mean rating also decreased. The weakest impression of a coherent motion was obtained at 25% correlated moving dots ($M = 0.45$, SEM = 0.08). However, the catch trials in which the subjects wrongly assumed to detect a target motion elicited an even weaker mean rating ($M = 0.19$, SEM = 0.07) if the subjects wrongly assumed to detect a motion. The analysis of variance revealed a highly significant effect of the level of coherence ($F(3,12) = 122.1$, $P < 0.001$, $\eta^2 = 0.97$). The test for trend supported the notion that the relationship between correlated motion signals and stimulus appearance can be described in linear terms (linear trend ‘Coherence’: $F(1,14) = 361.1$, $P < 0.001$, $\eta^2 = 0.96$).

The effect of a variation of the ‘SOA’ paralleled the effect of the level of coherence. Decreasing the SOA resulted in a reduction of the mean rating of the target motion—even

Table 1 – Median (MD) and mean (M) ratings of the strength of the perceived global motion

Level of coherence (in %) (SOA 300 ms)	Rating		SOA (in ms) (Coherence:100%)	Rating	
	MD	M (SEM)		MD	M (SEM)
25	0.38	0.45 (0.08)	0	2.21	2.06 (0.12)
50	1.40	1.47 (0.11)	100	2.31	2.24 (0.09)
75	2.30	2.39 (0.11)	200	2.70	2.73 (0.08)
100	3.04	3.03 (0.09)	300	3.04	3.03 (0.09)

The corresponding mean ratings were found to be increased when the percentage of local motion signal was increased (rows 1 and 2: ‘Coherence’), and the cue–target SOA, respectively (rows 3 and 4: ‘SOA’). Rating of catch trials not containing a target motion rarely exceeded ‘0’ ($P < 0.05$).

Catch trials (no coherent target motion): MD = 0.09, M = 0.19 (SEM = 0.07).

though its coherence remained constant at 100% (see Table 1). On the 5-point scale, the global motion was rated 2.06 (SEM = 0.12) at an SOA of 0 ms. The analysis of variance showed that the SOA had a significant effect which approximated the impact of the factor 'Coherence' with respect to the effect size ($F(3,12) = 15.95, P < 0.001, \eta^2 = 0.80$). Additionally, the statistical analysis revealed a linear relationship between the rating and the variation of the SOA between the cue and the target (linear trend 'SOA': $F(1,14) = 43.5, P < 0.001, \eta^2 = 0.76$).

2.2. ERPs

Due to the application of the RSVP techniques, the EEG recording was not only affected by the onset of the coherent target motion embedded in the motion RSVP stream but also by the repetitive changes of fixation color and the cue onset. Following a subtraction procedure established in previous experiments (Niedeggen et al., 2002, 2004; Rolke et al., 2001; Vogel et al., 1998), ERP signals related to the processing of the target were differentiated from ERP components triggered by the processing of the color cue. The following analyses of ERP waves are therefore based on 'difference waves', produced by subtracting the ERP signal triggered by the onset of the cue

alone (catch trials) from the ERP waves also containing brain responses to the target motion.

The grand-averaged difference waves extracted for the onset of a 100% coherent target motion at an SOA of 300 ms are depicted in Fig. 2. Since no significant deflections were obtained in the baseline period (-100-0 ms), the subtraction technique appeared to be efficient in order to eliminate the electrophysiological correlates related to the processing of the cue. Following the onset of the target motion, the ERP signal was dominated by a posterior negativity peaking at about 180 ms. The topography of the mean amplitude of this ERP component (temporal window: 150-200 ms) revealed a maximum at left posterior leads. This negativity - further labeled as N200 - is related to the sensory processing of motion onset (Bach and Ullrich, 1994; Kubová et al., 1995; Niedeggen and Wist, 1999). This component was followed by a positivity at occipital central leads, further labeled as P250. As defined in a temporal window extending from 225 to 275 ms, the topographical distribution of the mean amplitude of the P250 is less widespread as compared to the N200. Although the P250 component was also elicited in previous RSVP experiments (Niedeggen et al., 2002, 2004), its relation to motion processing has not been explored in detail. However, its onset latency indicates that this component

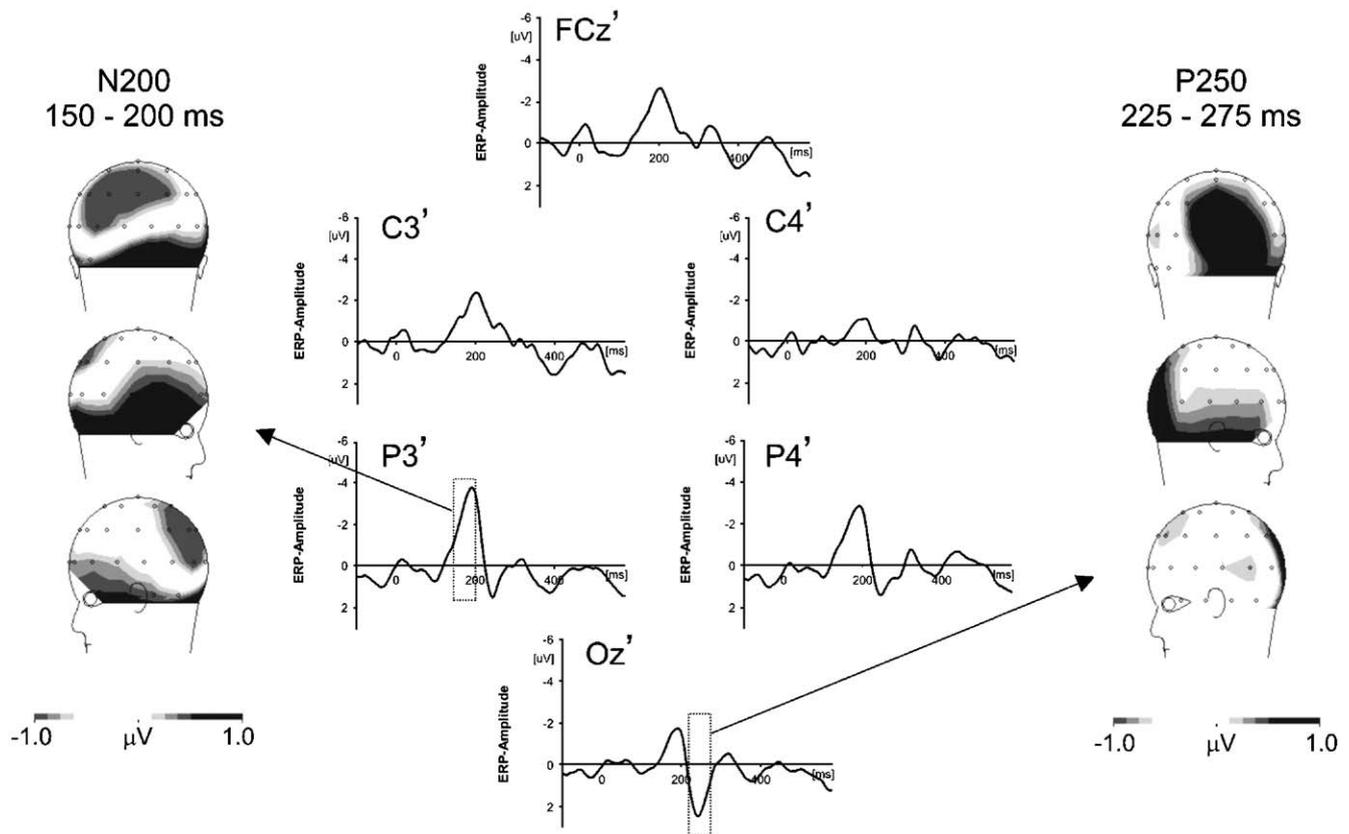


Fig. 2 – The grand-averaged ERP activity elicited by the onset of a coherent target motion (Coherence: 100% correlated moving dots; SOA: 300 ms). Effects of the processing of the color cue have been eliminated by subtracting the ERP signal obtained for catch trials (no coherent motion target). ERP traces are depicted for electrodes spatially approximating fronto-central (FCz', C3', C4') and parieto-occipital (P3', P4', Oz') standard positions. The average-referenced topographic map of the posterior negativity extending from 150 to 200 ms (N200) is shown in the left hand diagram. The corresponding distribution of the occipital positivity extending from 225 to 275 (P250) ms is shown in the right hand diagram. The maps are based on the average amplitudes obtained within the time windows selected.

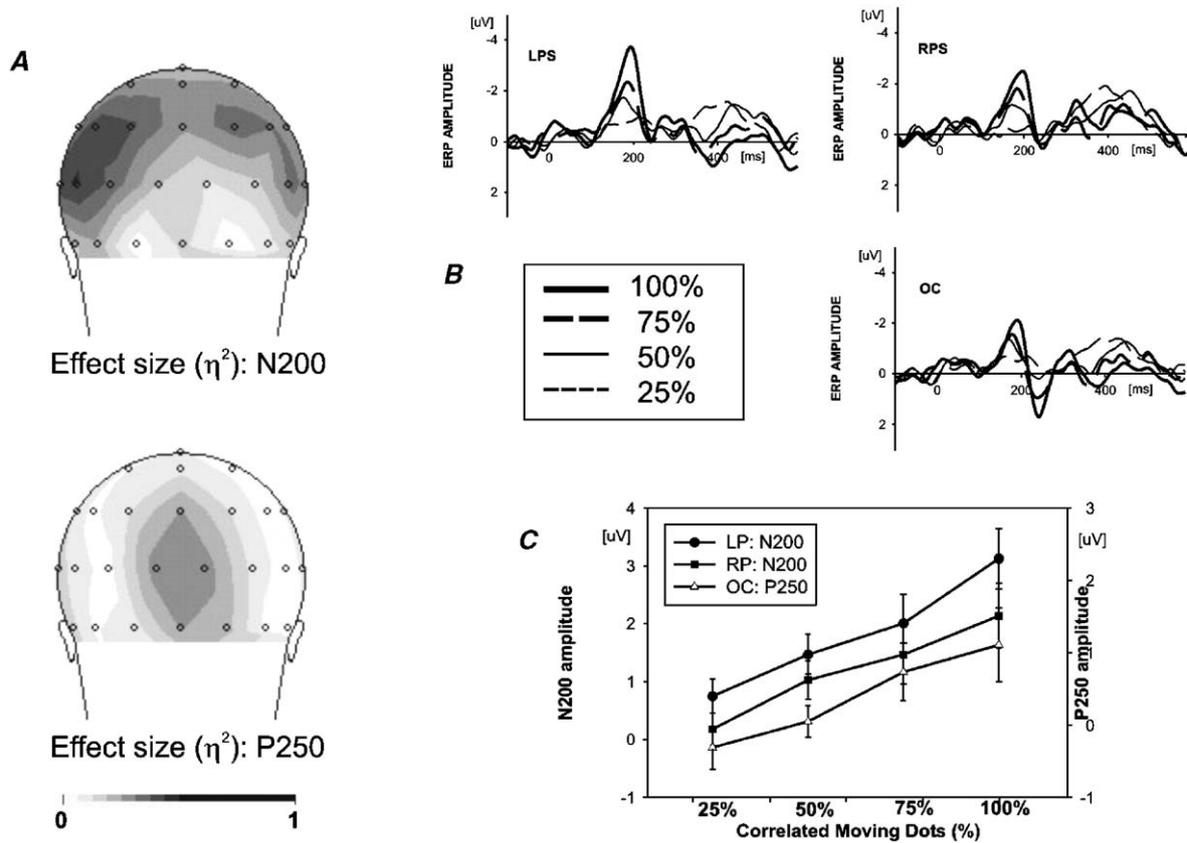


Fig. 3 – Experimental effect of the level of coherence: (A) spatial distribution of the effect size (η^2) for the N200 (top) and the P250 (bottom) amplitudes. The grey scaling indicated the extent at which the variance obtained at a single electrode can be attributed to the experimental effect of ‘Coherence’. For the N200 amplitude, left-parietal (LP) and right-parietal (RP) leads were most sensitive. For the P250 amplitude, sensitive electrodes were focussed at central occipital (OC) leads. (B) Grand-averaged ERP traces recorded at the three sensitive electrode clusters. ERP curves are superimposed for the four experimental conditions (25%, 50%, 75%, 100%). (C) Mean ERP amplitudes plotted as a function of the level of coherence. The mean N200 amplitude at left (LP) and right (RP) hemispheric clusters increased linearly with increasing percentage of correlated moving dots. The same was found for the P250 amplitude (OC). Error bars plot \pm SEM.

can probably be related to the processing of the offset of a coherent motion.

In the first step of the ERP analysis, the electrode cluster particularly sensitive to variations in the strength of the motion signal were identified. ‘Sensitivity’ was defined as a significant and reliable modulation in amplitude depending on the level of motion coherence. Therefore, for N200 and P250 amplitude at each electrode, a measure of the effect size of the factor ‘Coherence’, η^2 , was calculated separately. The spatial distribution of the effect size and the corresponding

definition of the electrode clusters are depicted in Fig. 3A. The ranked order of η^2 – determined for each electrode – identified the most sensitive electrodes in the temporal range of the N200 at left-parietal positions (cluster LP)¹. Averaging the effect sizes of the four adjacent electrodes revealed a mean η^2 of 0.65 (SEM = 0.04). In order to account for an effect of laterality, we also pooled the electrodes at homologous right-hemispheric positions (cluster RP)¹, in which the mean effect size was slightly reduced (mean η^2 = 0.55, SEM = 0.08). For the P250 component, the most sensitive cluster contained four electrodes positioned at occipital leads (Cluster OC: mean η^2 = 0.43, SEM = 0.02)¹. Because of the centered position of the electrodes, the factor ‘laterality’ was not considered.

In line with previous EEG and MEG results (Niedeggen and Wist, 1999; Nakamura et al., 2003), the N200 amplitude was found to be linearly dependent on the level of coherence of the motion signal (see Figs. 3B and C). The mean amplitude increased with increasing percentage of correlated moving dots from 25 to 100%. The analysis of variance confirmed a significant effect of the factor ‘Coherence’ ($F(3,12) = 4.44$, $P < 0.05$, $\eta^2 = 0.53$), which can be adequately described in

¹ Because of the equidistant positioning of electrodes embedded in the cap, single electrodes only approximate the positions defined in the ten-twenty-system. Therefore, the theta/phi coordinates are given for each cluster. Left parietal (LP) was defined by E1 (-58/60), E2 (-58/33), E3 (-86/54), and E4 (-86/30). Right parietal (RP) was defined by E5 (58/-60), E6 (58/-33), E7 (86/-54), and E8 (86/-30). Occipital (Oc) was defined by E9 (59/-90), E10 (86/-78), E11 (-86/78), and E12 (115/15). For each of the electrodes, the effect of the factor ‘Coherence’ was significantly as indicated by the MANOVA (mean P values: >0.001 for LP, 0.005 for RP, 0.011 for OC).

terms of a linear trend (test for linear trend 'Coherence' $F(1,14) = 15.43$, $P < 0.01$, $\eta^2 = 0.52$). The significant difference between the left- and the right-hemispheric cluster confirmed that the overall level of the mean amplitude was significantly lower at right-hemispheric clusters (factor 'Laterality': $F(1,14) = 8.59$, $P < 0.05$, $\eta^2 = 0.38$).

A similar relationship was identified for the P250 component (see Figs. 3B and C). As shown in the grand average ERPs, its amplitude was enhanced with increasing percentage of direction signals in the target motion. Whereas the effect of coherence was on the verge of significance in the multivariate analysis ($F(3,12) = 3.08$, $P = 0.068$, $\eta^2 = 0.44$), the test for trend clearly indicated a linear relationship (test for linear trend: $F(1,14) = 9.30$, $P < 0.01$, $\eta^2 = 0.40$).

Since the condition 'Coherence' served as a reference function, the same electrodes defined the clusters LP, RP, and OC when we tested the effect of the factor 'SOA'. As indicated in Fig. 4A, the mean effect size was found to be reduced: in the time range of the N200 (150–200 ms), the size of the effect was moderately expressed in the left posterior cluster (Cluster LP: mean $\eta^2 = 0.29$), but weakly in the right posterior cluster (Cluster RP: mean $\eta^2 = 0.09$). In the time range

of the P250, an effect of the experimental modulation was not obtained (Cluster OC: mean $\eta^2 = 0.02$).

Accordingly, a significant functional relation between the factor 'SOA' and the N200 amplitude depended on the laterality of the electrode cluster (factor 'SOA' × 'Laterality' ($F(3,12) = 3.71$, $P < 0.05$, $\eta^2 = 0.48$). As shown in Figs. 4B and C, the mean amplitude was larger at left-hemispheric leads, and the increase of SOA resulted in a steeper slope. If the statistical analysis was restricted to the left-hemispheric cluster, a significant effect of the SOA on the N200 amplitude was found ($F(1,14) = 5.00$, $P < 0.05$, $\eta^2 = 0.56$), as well as a linear increase of amplitude as a function of 'SOA' ($F(1,14) = 12.62$, $P < 0.01$, $\eta^2 = 0.47$).

In contrast, the amplitude of the P250 was not affected by the SOA between cue and target onset. Neither the multivariate analysis nor the test for trend revealed a significant relationship.

Figs. 5A–C summarizes the association between the targets' appearance and the ERP components. To estimate the predictive value of the ERP components on stimulus appearance, the correlation coefficients between the rating decision and the different ERP amplitudes (N200, P250) were

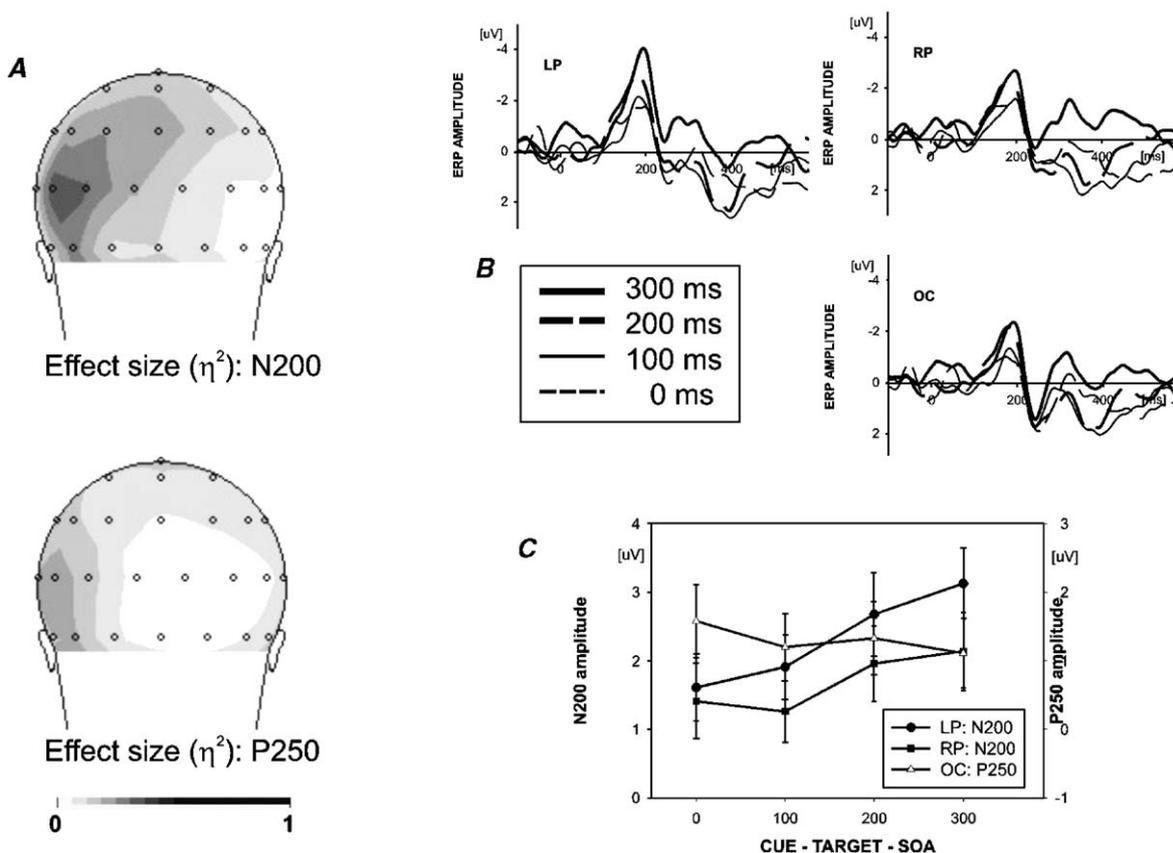


Fig. 4 – Experimental effect of the cue–target SOA: (A) spatial distribution of the effect size (η^2) for the N200 (top) and the P250 (bottom) amplitudes. The grey scaling indicated the extent at which the variance obtained at a single electrode can be attributed to the experimental effect of 'SOA'. For the N200 amplitude, the sensitivity of the previously defined left-parietal cluster (LP, see A) was confirmed. In contrast, the P250 was obviously not affected by the experimental manipulation. (B) Grand-averaged ERP traces recorded at the three predefined electrode clusters. ERP curves are superimposed for the four experimental conditions (0, 100, 200, and 300 ms). (C) Mean ERP amplitudes plotted as a function of the cue–target SOA. The mean N200 amplitude at the left-hemispheric cluster (LP) increased linearly with increasing cue–target SOA, however, the P250 amplitude was not affected. Error bars plot \pm SEM.

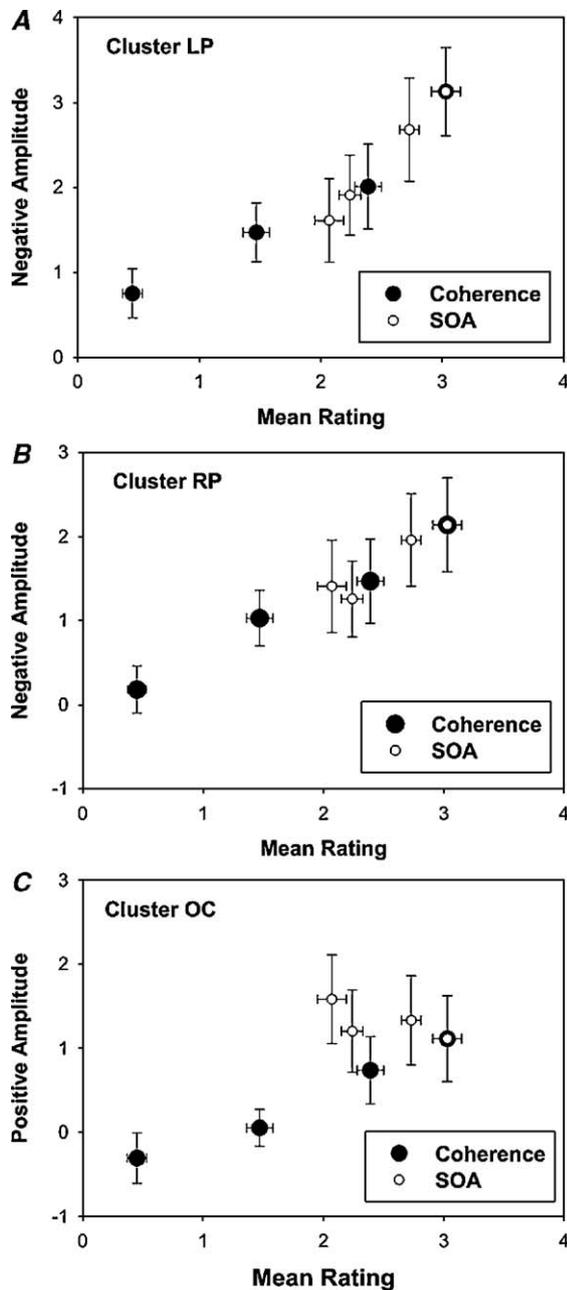


Fig. 5 – Correlation of the mean psychophysical rating and the mean ERP amplitudes. The effects of the ‘physical’ (level of coherence: closed circles) and the ‘attentional’ (SOA: open circles) manipulations are separated in each figure. (A) The N200 amplitude at the left-parietal leads (LP) was associated with the perceived global motion—independently of the experimental manipulation. (B) The N200 amplitude at right-hemispheric leads (RP) serves as a predictor for target appearance in the ‘Coherence’ rather than in the ‘SOA’ condition. (C) The P250 amplitude at occipital leads (OC) is only related to the perceptual strength when the level of coherence is varied. Error bars plot \pm SEM.

computed in each subject. For the N200 amplitude in the cluster LP (Fig. 5A), the mean correlation coefficient was at -0.48 (SEM = 0.14) for the condition ‘Coherence’ and at -0.56

(SEM = 0.12) for the condition ‘SOA’. A statistical comparison based on the individual coefficients (Fisher z-transformed) did not reveal a significant difference between the two factors ($t(14) = -0.76$, $P = \text{n.s.}$). At right-hemispheric leads, the predictive value of the ERP amplitudes was reduced in both conditions (‘Coherence’: $M = -0.49$, SEM = 0.14; ‘SOA’: $M = -0.38$, SEM = 0.16), and a significant difference was not obtained ($t(14) = -0.52$, $P = \text{n.s.}$). In contrast, the P250 amplitude was related to the subjects’ rating if the level of coherence was modulated ($M = 0.41$, SEM = 0.16), but not the cue–target SOA ($M = 0.00$, SEM = 0.17). The statistics confirmed that the P250 amplitude served as a predictor for stimulus appearance in the condition ‘Coherence’, but not in the condition ‘SOA’ ($t(14) = 2.59$, $P < 0.05$).

3. Discussion

3.1. Summary of the results

Our main findings can be summarized as follows: (1) the appearance of a correctly detected target motion – defined as the perceived strength of a global coherent motion – can be modulated by both, the physical stimulus properties as defined by the percentage of correlated moving dots, and by the cue–target SOA in a temporal selection task. (2) For both manipulations, a common electrophysiological correlate can be identified. The amplitude of the N200 component increased with increasing the percentage of coherently moving dots, but also reflected the modulation in perceived motion strength of a fixed physical target in a RSVP task. (3) A subsequent occipital component, the P250, was related to the variation of motion coherence but did not reflect the variation in stimulus appearance caused by the temporal distance between cue and target.

3.2. Psychophysical effects of physical and SOA modulation

The rating of the perceived motion strength decreased gradually with decreasing cue–target SOA. The process which modulates the targets’ appearance as a function of cue–target SOA is likely to be related to the costs of processing the color cue or to the deployment of attention from the local to the global RSVP stream. Following the idea of a psychological refractory period (PRP) (Pashler, 1994), the processing of a secondary target may be affected when general processing capacity is shared between tasks at short SOAs. According to a hybrid model of attention (Lavie, 1995), the processing load induced by the color selection task restricts the capacity for motion processing. With increasing SOA, more capacity will be released for the ‘secondary task’, which is the evaluation of the motion target. Alternatively, restrictions in the processing of the motion target may also result from the spatial re-direction of the attentional focus (Eriksen and Murphy, 1987). However, the latter explanation cannot account for the monotonic increase of the perceived strength in the range of the SOA tested (0–300 ms). Given the high validity of the color cue and the spatial distance from local to global

stream, the time necessary to shift attention should not exceed 100 ms (Tsal, 1983). Therefore, it is more likely to assume that attentional resources will have to be re-distributed within the visual system.

Overall, our results are in line with earlier psychophysical findings based on visuospatial tasks demonstrating that attentional deployment as well as perceptual load affect the appearance of visual stimuli (Carrasco et al., 2004; Prinzmetal et al., 1997, 1998; Tsal et al., 1994).

3.3. SOA effects on the N200

The ERP data are in line with our previous findings (Niedeggen et al., 2002) which showed that the N200 amplitude increased with increasing cue–target SOA. Moreover, the N200 amplitude was confirmed as a reliable predictor for stimulus appearance. The relationship between the N200 and the psychophysical rating does not only hold for the variation of the ‘physical’ input (level of coherence) but also for the modulation of the cue–target SOA.

Earlier MEG studies have identified the neural generator of the N200 in the motion-sensitive extrastriate cortex V5 (Nakamura et al., 2003). Furthermore, the hemodynamic activity of this area was found to vary monotonically with the level of coherence (Heeger et al., 2000; Rees et al., 2000) which also parallels the properties of the N200. Given that the N200 reflects the activation at a sensory level of visual processing, our findings support the notion that the effect of attention on stimulus appearance is mediated on the level of early visual processing (Carrasco et al., 2004).

This conclusion is also in line with earlier ERP findings demonstrating that attentional capacity modulates the neural activity at an early sensory level (Mangun and Hillyard, 1990; Parasuraman, 1990). In these studies, the amplitude of the sensory ERP components increased progressively with shifting the task priority. Since the simultaneous activation of non-overlapping sensory areas (i.e., color and motion) requires the sharing of common attentional resources (Just et al., 2001; Rees et al., 1997; Vandenberghe et al., 1997), it is likely that a similar effect is induced with increasing the cue–target SOA in our temporal selection task.

Although the re-distribution of attentional resources can account for the effects on perception and sensory ERP components, the question on the neural mechanism involved remains open. One might argue that the attentional resources available affect the signal-to-noise ratio within the motion-sensitive system (Huk and Heeger, 2000). On the other hand, the shift of resources might affect the temporal integration of the motion signal which determines the perceptual decision (Mazurek et al., 2003). Both processes are compatible with the reduction of the N200 amplitude as a function of cue–target SOA.

3.4. SOA effects on the P250

In contrast to the N200 component, the functional significance of the late occipital component, labeled as P250, is not established. The occipital focus of the topography parallels the topography of the P100 elicited by contrast reversal and indicates its origin in the primary visual cortex (Hashimoto et

al., 1999; Seki et al., 1996). In contrast to the P100, the P250 is associated with the processing of motion signals as confirmed by its correlation with the factor ‘level of coherence’. On the basis of its topography and functional characteristic, we would like to propose that the P250 indexes the end of the global motion episode (target) and its transition to a random walk sequence. This is in line with fMRI studies reporting that the primary visual cortex is better activated by the onset of uncorrelated motion signals (global ‘noise’) in contrast to coherent motion (Braddick et al., 2001).

Although the P250 is related to the processing of visual motion, its amplitude does not depend on the cue–target SOA. This finding is interesting in two respects. Firstly, it may be that certain motion features can be processed independently of attentional limitations (Dick et al., 1987; Nakayama and Silverman, 1986). Secondly, it shows that the subtraction method applied ($ERP[\text{target} + \text{cue}] - ERP[\text{cue}]$) does not produce a methodological artefact. If the processing of the cue and the target activates a common neural system, the refractory period of ERP components would have to be considered (Nelson and Lassman, 1973; Woods et al., 1980). Accordingly, the ERP response to the second stimulus depends on the temporal distance to the first stimulus. However, the motion-sensitive P250 was not modulated by the cue–target SOA indicating that the processing of the color cue did not induce a refractory period for motion processing in general.²

3.5. Does target appearance determine target detection?

Although the current paper focuses on the processing of target stimuli correctly detected by an observer, its results raises the question whether the effect of SOA on sensory processing and stimulus appearance also contributes to the phenomenon of motion blindness obtained in previous experiments (Sahraie et al., 2001). Such an interaction implies that visual awareness is a gradual phenomenon primarily defined by the quality of the sensory representation (Kanwisher, 2001). On the other hand, it is not congruent with the idea of a stochastic all-or-none character of conscious perception (Sergent and Dehaene, 2004) which has been supported in the ERP studies on the attentional blink (Vogel et al., 1998; Rolke et al., 2001).

Although our data show that sensory processing and stimulus appearance are significantly correlated in a temporal selection task, it is unlikely that conscious detection of the target is entirely defined by quality of the targets’ sensory representation for the following reasons. Firstly, the effect of stimulus appearance as a function of cue–target SOA did not depend on the frequency of motion distracters (irrelevant coherent motion epochs preceding the onset of the cue).

² Although the subtraction methods did not produce a methodological artefact by affecting the expression of motion-evoked responses per se, the re-distribution of the attentional resources from the color to the motion system cannot be accurately traced. In order to isolate the shifting effect by means of ERPs, the cue will have to be presented in a different sensory modality (i.e., auditory cue). This will reduce the probability that the sensory responses to cue and target overlap with respect to their onset and topography. However, such a manipulation might also affect the necessity to re-distribute resources (Rees et al., 2001).

Although our previous studies have shown that subjects' hit rate depends on the number of distracters (Hesselmann et al., 2006), a control experiment revealed that distracter frequency does not affect the mean rating of the motions strength. Secondly, the reduction in stimulus appearance with decreasing SOA did not approach the coherence threshold. A linear interpolation of the psychophysical data obtained in our 'Coherence' condition indicates that a coherent target motion (100% correlated moving dots) was perceived as a target motion of 61% correlated moving dots at a SOA of 0 ms. Such a coherence signal clearly exceeds the motion coherence threshold which is about 10% correlated moving dots (Vaina et al., 1990). Therefore, our data support a 'late selection' account in temporal selection tasks with respect to the conscious representation of the target stimulus and not with respect to its sensory representation.

3.6. Conclusion

In sum, our data provide evidence that stimulus appearance cannot only be modulated in visuospatial (Carrasco et al., 2004; Tsal et al., 1994) but also temporal selection tasks. The correlation between the subjects' impression and the N200 amplitude suggests that the effect site can be localized at a sensory level of processing. In turn, the N200 was established as a reliable predictor for the subjects' perceptual state. A comparable conclusion has been drawn from single unit recordings in area MT/V5 (Salzman and Newsome, 1994).

We also found that the modulation of the targets' appearance as a function of SOA is unlikely to contribute to the effect of transient motion blindness previously reported (Sahraie et al., 2001). The conscious representation of the target appears to be determined by the degree of a central suppression rather than the neural activity at sensory level (Niedeggen et al., 2002, 2004).

4. Experimental procedure

4.1. Observers

A total of 15 naïve observers (7 female, 8 male) aged between 23 and 35 participated in the ERP study. All subjects were recruited and tested at the University of Düsseldorf. They had normal or corrected-to-normal visual acuity, no history of neurological disorders and were naïve with respect to the purpose of the study.

4.2. Stimuli

The setup of the visual stimuli and the sequencing is outlined in Fig. 1A. The stimulus contained a 'global' motion and a 'local' color RSVP stream and was displayed on an SVGA monitor using a VSG stimulus generator (Cambridge Research Systems, UK). The global stream consisted of 400 randomly distributed white dots ($0.18 \times 0.18^\circ$; 146 cd m^{-2}), moving at $13.5^\circ \text{ s}^{-1}$ within a grey square ($25 \times 25^\circ$, 19.2 cd m^{-2}), sparing an inner circle of lighter grey (diameter 3.5° , 31 cd m^{-2}). The local stream was defined by the fixation point (0.5° in diameter) positioned in the center of the inner circle.

In each trial, lasting 5 s, the color of the grey fixation point (19.2 cd m^{-2}) was randomly changed for 100 ms to green, blue, yellow, or red. The mean frequency of color changes was about 33% (~15 episodes per trial). The peripheral dots defining the global stream were constantly in motion throughout the trial. Most of the time the peripheral dots moved in a random walk, in which the individual direction of each dot was randomly assigned every 10 ms. For distracter motion stimuli, the global uncorrelated motion was occasionally interrupted for 100 ms when all the dots moved in one of the four cardinal directions (up, down, left or right, defined 100% correlated moving dots). The onset of a color change was independent from the onset of the coherent motion episode, with exception of the cue and target (see below). Care was taken to ensure that two successive coherent episodes always differed in their direction of movement.

4.3. Task and design

The subjects were instructed to fixate on the fixation point for the duration of each trial and to watch attentively for the single presentation of a red fixation (cue), which occurred at random between 2 and 3.5 s after the start of the trial. The red cue was the signal to detect an episode of coherent motion (target) in the global stream. Coherent motion episodes prior to the onset of the cue had to be ignored. To reduce selection errors, the interval between the last irrelevant coherent motion and the onset of the cue was at least 500 ms, and no further episodes of coherent motion occurred after the target.

In contrast to our previous experiments on motion blindness (Sahraie et al., 2001; Niedeggen et al., 2002, 2004), the design was changed in two respects: the direction of the target motion was constant (upwards), and the subjects were asked to rate the strength of the perceived target motion on a 5-point scale. The scale was visible following the offset of each trial at the bottom of the monitor display and ranged from '0' (very weak coherent motion detected) to '4' (strong coherent motion detected). The appropriate values were selected with a response button. Subjects were provided with an additional button to indicate that the target motion was not detected.

The experiment included two blocks of training: In the first block, the SOA between cue and target was held constant at 300 ms, and the percentage of correlated moving dots was varied in four steps (levels of coherence: 25, 50, 75, and 100%). Subjects learned to discriminate between the four different motion strengths. Targets of each coherence level were presented for 10 times each, and the same number of catch trials (no coherent target) was included. The total of 50 trials was presented in randomized order. The frequency of coherent distracter motions presented before cue onset was about 33% (~6 episodes/trial). To increase the discrimination ability, feedback was provided. If an observer failed to discriminate the coherence levels reliably, the first block was repeated. In the second block, the temporal distance between the cue and target was additionally varied in four steps (SOA: 0, 100, 200, and 300 ms). For each SOA, each level of coherence (25, 50, 75, 100%) was presented five times. Together with the catch trials ($n = 20$), a total of 100 trials was presented. The trials were presented in randomized order. Subjects were

informed that the temporal interval between the cue and the target was variable. No feedback on the rating performance was provided in the second block of training.

The main experiment study comprised the factors ‘Coherence’ and ‘SOA’. At a SOA of 300 ms, coherence of the motion target was varied in four degrees (25, 50, 75, and 100% correlated moving dots). Holding the coherence of the target constant at 100%, the cue–target SOA was varied in three further degrees (0, 100, and 200 ms). The incomplete design was justified because we analyzed the effects of ‘Coherence’ and ‘SOA’ on the perception of global motion separately. Furthermore, pilot studies showed that the rating behavior for the function ‘SOA’ (0–300 ms, target: 100% coherence) was not affected by the presence or absence of additional targets with a lower level of coherence (25–75%) in the same SOA range. Additional 60 catch trials were presented in order to estimate the ERP response to the onset of the cue. In total, the ERP experiment comprised 480 trials. The sequence of conditions was randomized.

Subjects were not informed that the coherence of the target motion at short SOAs was held constant. As in the training trial, the frequency of coherent distracter motions presented before cue onset was about 33% (~6 episodes/trial). Eye movements and blinks were allowed in the inter-trial interval which was terminated by the subject’s response. Following a rating response, the next trial was started with a time delay of 1 s.

4.4. EEG recording and data analysis

An elastic cap with predefined and equidistant electrode positions (Falk-Minow-Services, Munich) was mounted on the subject’s head. The 45 active silver–silver chloride electrodes were referenced to linked mastoids, with impedance kept below 5 k Ω . Additional electrodes attached at the outer canthi and the sub- and supraorbital ridges of the right eye controlled for horizontal (hEOG) and vertical (vEOG) eye movements. EEG signals were recorded continuously with six 8-channel ‘EEG-8’ amplifiers (Contact Precision, London). Data were bandpass-filtered online (0.03 to 200 Hz) and sampled at 250 Hz. Offline, EEG data were segmented according to the onset of the cue in each trial (–100 to 1200 ms epoch length), filtered (0.5–40 Hz, –24 dB cut-offs), and baseline corrected (–100 to 0 ms before cue onset). Single EEG sweeps containing muscular or ocular (vEOG, hEOG) artefacts were excluded from the analysis. The remaining sweeps were separately averaged for the active electrodes according to the experimental conditions (‘level of coherence’: 25%, 50%, 75%, and 100%; ‘SOA’: 0, 100, 200, and 300 ms). To isolate the response to the motion target, the averaged response obtained in the catch trials (color cue, no motion) was subtracted. The percentage of rejected trials never exceeded 15% in any subject. Thus, averages were always based on a minimum of 40 trials.

Averaged ERP data were characterized by two components identified by means of the global field power (Lehmann and Skrandies, 1979). The negative peak (N200) was described in terms of the mean amplitude obtained between 150 and 200 ms, the following positivity (P250) covered the time range from 225 to 275 ms.

For each component, a cluster of four adjacent electrodes was defined which was significantly sensitive to a variation of motion coherence. For this reason, the effect size of the factor ‘Coherence’ (η^2) was calculated for the amplitudes at each electrode. The effect size indicates the proportion of the total variance that is attributed to an effect (Kirk, 1982). On the basis of the ranked order of effect sizes, we identified for each ERP component a cluster containing four electrodes. Additionally, we made sure that each of the electrodes was significantly affected by a variation of the strength of the motion signal ($P < 0.01$)¹. Please note that the clustering procedure did not imply a correlation between the experimental factors (Coherence, SOA) and the ERP amplitude.

Based on the mean amplitudes calculated in these clusters we determined the statistical effects of ‘Coherence’ and ‘SOA’ running a multivariate analysis of variance (Pillai-Spur-Test, SPSS for Windows, Version 11.0). Additional tests for trends were computed to describe the dependence of ERP amplitudes as a function of motion coherence and SOA, respectively. The same statistical procedures were applied to analyse the psychophysical effects of the rating. Only those trials were considered in which the target has been detected correctly. Since the direction of the target motion was predefined, misses of the motion target occurred rarely (<10%).

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