

Research report

Repetition related ERP effects in a visual object target detection task

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Abstract

ERP responses to initial and repeated presentations of possible and impossible objects were recorded from 61 recording sites in a simple target detection task. In Experiment 1, the non-target objects were line drawings of possible and impossible 3-D geometric figures and the targets were line drawings of familiar everyday objects or combinations of parts of everyday objects. In Experiment 2, the non-target objects were everyday objects and the targets were possible and impossible 3-D geometric figures. In both experiments, at frontal sites, the repeated possible and impossible non-target items elicited less negative ERP waveforms relative to first presentations between 250 and 350–400 ms. At parieto-occipital sites, in both experiments, the repeated possible and impossible non-target items elicited less positive ERP waveforms than did first presentations beginning at about 300 ms. The briefly reduced frontal negativity to repeated items is consistent with familiarity arising from a facilitation of access to conceptual, semantic and visuo-spatial representations during object categorization. The polarity of the parieto-occipital effect was the reverse of what is usually found in stimulus repetition tasks, although it is consistent with earlier work using similar visual stimuli. It is interpreted as reflecting the availability of a newly formed representation (i.e., token) of the object just experienced. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Neural basis of behavior

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1. Introduction

ERP waveforms elicited by repeated stimuli are usually more positive than the ERP waveforms elicited by initial presentations (for reviews see [30,42]). Stimulus repetition can either be task relevant in that the participant is required to indicate whether an item has been presented previously in the experimental session (recognition paradigms), or task irrelevant in that the task does not require the participant to indicate, or even be aware, that the item has been presented previously (e.g., lexical decision, semantic categorization, target detection).

A number of authors have interpreted the increased positivity seen in the ERP waveform to repeated stimuli as a modulation of at least two distinct components: a reduction in the amplitude of the N400, a negative going

waveform that peaks around 400 ms, and an increase in the amplitude of a late positive component [7,25,43,59] (see [24] for a discussion of multiple subcomponents). Indeed, modulations of either an early negative component, a late positive component, or both, have been reported in recognition and repetition paradigms that used linguistic materials [3–7,14,26,34–37,43–45,47–49,53,54,57,59,60], and non-linguistic materials such as line drawings and pictures of everyday objects, faces, patterns, geometric shapes, as well as environmental sounds [3,11,12,15,31,32,38,40,50,60].

However, there are some notable exceptions to the general characterization of ERP repetition effects as an attenuation of an early negative component and the enhancement of a late positive component. For example, several studies using word stimuli have shown a reduction in the late positive component with stimulus repetition when items were repeated after a supporting semantic context, i.e., a sentence, rather than in a list of isolated items [7,59]. In addition, at least two studies using visual stimuli (patterns or line drawings and pictures of objects)

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have also found decreased positivity to repeated stimuli [50,60].

In the present study, we focus on effects of stimulus repetition when repetition itself is not relevant to the task requirements. ERP repetition effects in this type of paradigm have been attributed to a number of different cognitive processes. For example, Bentin and McCarthy [3] suggested that in immediate repetition classification tasks, such as lexical decision and familiar–unfamiliar face discrimination, the ERP effect related to repetition, i.e., increased positivity for repeated items, reflects the elimination of the need for stimulus analysis processes, including access of semantic memory, and the consequent speeding of the categorical decision process, due to the involvement of episodic memory for the previous classification decision. Consistent with this view, tasks that can be completed on the basis of shallow perceptual analysis, such as face/non-face discrimination and word/number discrimination, and that do not require or evoke access to semantic memory do not elicit a repetition effect [3].

Rugg and colleagues [46,49,50] provided an alternative explanation of the ERP repetition effect. They suggested that it reflects easier integration of repeated information into its proper context, and that this reduced processing effort for integration applies only to information that can be represented in a unitized code, i.e., ‘encoded at a level of abstraction beyond that of its surface features’, such as a lexical, semantic, or episodic representation [46,49,50]. The failure of stimuli such as orthographically illegal non-words [49] or nonsense figures consisting of several unconnected lines [50] to elicit a repetition effect occurs, according to this model, because the information is not represented in a unitized code.

Support for the claim that the repetition effect reflects facilitation of processing from a number of different representational formats includes data from a target detection experiment that used line drawings of 3-D geometric objects [50]. The 3-D line drawings were modeled after figures used by Schacter, Cooper and their colleagues to study object representation (e.g. [52]), and did not have any inherent semantic meaning as such. Therefore, contrary to the Bentin and McCarthy interpretation, it seems unlikely that the repetition effect reflects only facilitated access to semantic memory. Interestingly, the ERP repetition effect elicited by these 3-D geometric objects was polarity reversed, i.e., the repeated stimuli elicited less positive waveforms than the initial presentations in both an early time window (200–400 ms) showing a parietal maximum and a later time window showing a frontal maximum (400–900 ms). Rugg et al. suggested that in their experiment the reversed polarity may have been due to involvement of cortical cells with a different orientation from those activated when word or number stimuli are used. An alternative explanation is that the reduced positivity reflects a reduction in neural activity elicited by repeated stimuli relative to first presentations. Indeed, a

number of neuroimaging studies have shown blood flow reductions with stimulus repetition in implicit memory tasks [1,9,10,41,51,56] (see [63] for review). Additionally, single unit recordings in the macaque monkey have shown a class of neurons that reduce their firing rate when stimulus repetitions occur [13,33]. Similar changes in human neuronal activity to repeated stimuli could underly the neuroimaging results as well as the putative reductions in neural activity as measured by ERPs [63].

The present study addressed two issues. One, the stimulus specificity of the polarity reversed repetition effect reported by Rugg et al. [50] was examined by using both line drawings of 3-D geometric figures (Exp. 1) and line drawings of everyday objects (Exp. 2). If, as suggested by Rugg et al., the ERP repetition effect was polarity reversed because the orientation of the generating tissue depends on stimulus characteristics, e.g., words vs. geometric objects, then the stimuli used may modulate the polarity of the repetition effect. The everyday objects have semantic meaning and a verbal label as well as visuo-spatial features. Therefore, these objects may elicit the more typical ERP repetition effect. Two, impossible objects, both line drawings of objects that could not exist as 3-D structures in the real world (Exp. 1) and nonsensical combinations of everyday object parts (Exp. 2), were used to determine if the absence of an immediate repetition effect reported for nonsense patterns [50] is generalizable to conceptually and/or structurally impossible objects.

2. Methods

2.1. Experiment 1

2.1.1. Subjects

Twenty-two volunteers from the University of Leipzig (11 female) between 17 and 27 years of age (mean=22) participated in return for cash payment. All participants were right-handed and had normal or corrected to normal vision.

2.1.2. Apparatus

All stimuli were presented on a 17 inch VGA monitor under the control of a personal computer. Participants sat in an acoustically and electrically shielded dimly lit chamber at a viewing distance of approximately 120 cm from the monitor. Participants responded to the target stimuli using a custom built three-button response pad.

2.1.3. Stimuli

Target stimuli consisted of 34 figures, drawings of real world objects such as a hammer and a sailboat from the Snodgrass and Vanderwart pool [55]. An additional 34 target stimuli were scrambled figures, drawn by combining selected features from other, unrepresented, figures from Snodgrass and Vanderwart. For example, a figure might

consist of part of a piano attached to a section of an automobile and an elephant's leg.

Non-target stimuli consisted of 224 line drawings of possible and impossible geometric objects. Possible objects are objects whose surfaces and edges are connected in such a way that they could potentially exist in the real world whereas impossible objects contain subtle surface, or contour violations that would make it impossible for them to exist as 3-D objects [52].

2.1.4. Procedure

All participants were tested individually. There was an initial 14 trial practice phase. Two trials were target trials, eight trials were initial presentations of non-target stimuli (four possible and four impossible geometric figures), and four trials were immediate repetitions of non-target stimuli. Following a brief pause the test-phase began. There were 68 target trials (34 possible and 34 impossible real-world figures), and 336 non-target trials. The non-target trials consisted of 112 figures presented once only, and 112 figures that were presented twice with the second presentation immediately following the first. Half of the non-target figures were possible and half were impossible. The task is illustrated in Fig. 1.

Stimuli were presented for 500 ms each with a 1200 ms offset to onset delay between stimuli. Stimulus presentation order was pseudo-random with the constraint that

repeated stimuli followed immediately after the first presentation. Prior to the practice phase, participants were shown examples of target and non-target stimuli. Participants were told to press the right and left response buttons with their right and left thumbs in response to targets and to withhold responding for non-targets. No mention was made of the distinction between the possible and impossible non-target objects. The repeated non-targets for 11 participants were the non-repeated non-targets for the other 11 participants.

2.1.5. ERP recording

The EEG activity was recorded with Ag/AgCl electrodes, mounted in an elastic cap (Electrocap International), from 61 scalp sites of the extended 10–20 system. The C2 recording site served as the ground electrode. The electro-oculogram (EOG) was recorded from electrodes positioned at the outer canthus of each eye and just below the left eye. Electrode impedance was kept below 5 kOhms. The right mastoid was actively recorded as an additional channel. All scalp electrodes were referenced to the left mastoid and were off-line re-referenced to both mastoids. The EEG and EOG were recorded continuously with a band pass from DC to 70 Hz at a sampling rate of 250 Hz.

ERPs time-locked to stimulus onset were computed for each participant at all recording sites using epochs extend-

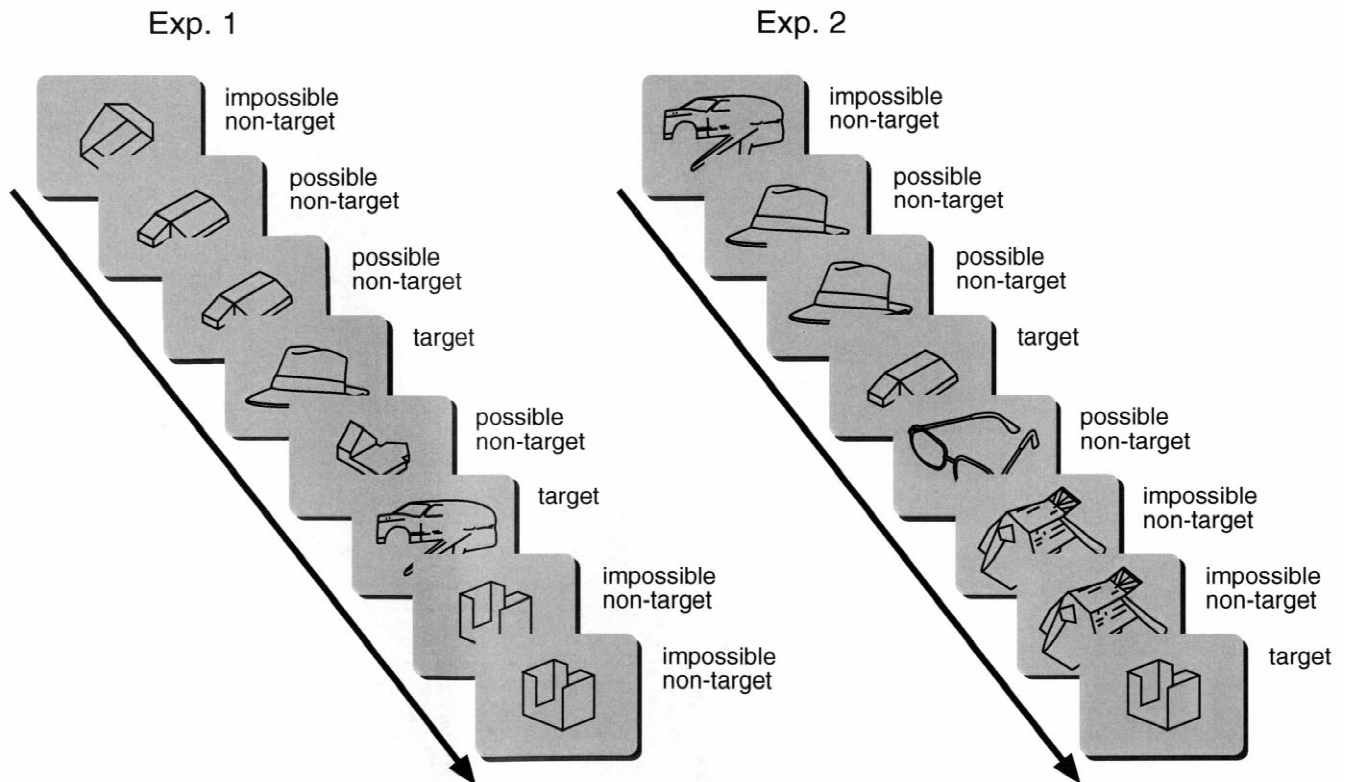


Fig. 1. Task design for Experiments 1 and 2. Stimuli were presented for 500 ms each with an ISI of 1200 ms. Only target stimuli required a response and repetitions, when they occurred, had a lag of zero items.

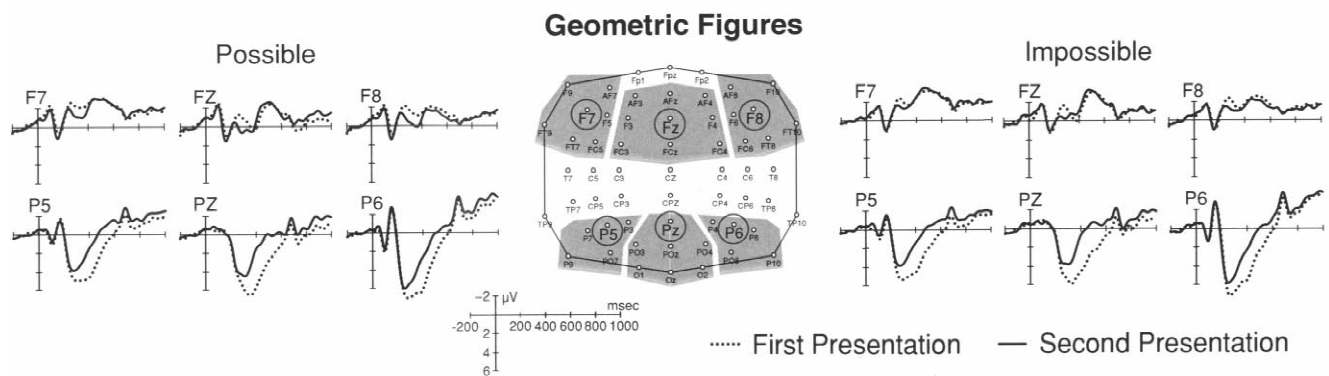


Fig. 2. ERP waveforms, averaged across subjects, elicited by the first and second presentations of possible (left side) and impossible (right side) geometric figures. The electrodes contributing to the frontal and parietal regions of interest (ROIs) lie in the shaded areas. Waveforms are plotted for one electrode from each of the six ROIs. Time is on the *x*-axis (ms) and voltage is on the *y*-axis (μ V, positive down). Only correct trials were included in the averages.

ing from 200 ms before stimulus onset to 1000 ms thereafter. The ERPs elicited by correctly classified stimuli (responded targets and non-responded non-targets) were selectively averaged according to item type (first or second presentation of a possible or impossible non-target; target). The 200 ms preceding stimulus presentation served as a baseline. Epochs contaminated by EOG or other artefacts were excluded from the averaging procedure.

Electrode sites were pooled to form six topographical regions of interest, as illustrated in Fig. 2 (ROIs: Left-frontal: F9, AF7, F7, F5, FT9, FT7, FC5; Medial-frontal: AF3, AFz, AF4, F3, Fz, F4, FC3, FCz, FC4; Right-frontal: AF8, F10, F8, F6, FC6, FT8, FT10; Left-parieto-occipital: P3, P5, P7, P9, PO7; Medial-parieto-occipital: Pz, PO3, POz, PO4, O1, Oz, O2; and Right-parieto-occipital: P4, P6, P8, P10, PO8). According to Homan, Herman, and Purdy [21], who established a correspondence between electrode site and underlying cerebral structures using radiographic techniques, the medial frontal region is approximately over the middle frontal gyrus (Brodmann area, BA, 46). The left and right frontal regions are approximately over the inferior frontal gyri (BA 45, 46). The left and right parieto-occipital regions cover approximately the posterior part of the middle temporal gyri and the anterior occipital sulcus (BA 19, 37) whereas the medial parieto-occipital region is approximately over the gyri occipitales and the superior parietal lobe (BA 17, 7). However, it is important to note that because of volume conduction of electrical potentials in the brain an ERP effect recorded at a particular electrode location was not necessarily generated by the cortical tissue lying immediately below that location.

ERPs were quantified as mean amplitudes within specific time windows in each of the ROIs. Repeated measures ANOVAs with factors Laterality (left vs. medial vs. right), and Repetition (repeated vs. non-repeated) were performed separately for possible and impossible objects and separately for frontal and parieto-occipital ROIs. The non-repeated level of the factor Repetition consisted

exclusively of first presentations of a repetition pair, items presented once only were not included¹ in the statistical analysis. As the Laterality factor is only of interest when it interacts with the Repetition factor it is not reported as a main effect. All effects with two or more degrees of freedom in the numerator were adjusted for violations of sphericity according to the Greenhouse–Geisser formula [18]. Scalp potential topographic maps of selected ERP results were generated using a 2-D spherical spline interpolation [39] and a radial projection from Cz, which respects the length of the median arcs.

2.2. Experiment 2

2.2.1. Participants

Nineteen volunteers from the University of Leipzig (9 female) between 18 and 29 years of age (mean=22) participated in return for cash payment. All participants were right-handed and had normal or corrected to normal vision.

2.2.2. Apparatus

Same as Experiment 1.

2.2.3. Stimuli

Target objects were drawn from the set of line drawings of possible and impossible geometric figures that were

¹To ensure that any ERP differences were due to differences between first presentation and immediate repetition of items we restricted our analysis to items that were actually repeated. Comparison of the waveforms for first presentations of repeated and non-repeated stimuli did not reveal statistically significant differences at the frontal or parietal ROIs for the possible objects in Experiment 1 or 2. For the impossible objects there was no difference at frontal sites in Experiments 1 and 2 or parietal sites in Experiment 2, but the first presentations of repeated items were more positive than the first presentations of non-repeated items. However, the reported difference between first and second presentations of repeated items held when the comparison was between non-repeated items and second presentations.

used as non-targets in Experiment 1. There were 34 possible targets and 34 impossible targets. A set of 112 possible everyday [55] figures and 112 scrambled everyday figures served as the non-target objects.

2.2.4. Procedure

The procedure was the same as in Experiment 1 with the exception that geometric figures served as targets and real-world figures served as repeated and non-repeated non-targets. The task is illustrated in Fig. 1.

2.2.5. ERP recording

As in Experiment 1.

3. Results

3.1. Experiment 1

3.1.1. Behavioral performance

The group mean proportion of correctly identified stimuli, presented in Table 1, indicates that performance was excellent in this task. On average, participants made fewer than 1% false alarms to possible and impossible objects on both first and second presentation and more than 99% of targets of both types were identified correctly. A 2-way ANOVA was conducted on the proportion correct responses to non-target items with Object Type (Possible, Impossible) and Repetition (1st and 2nd presentation) serving as repeated measures factors. For the non-target objects there was no significant effect of Object Type, $F(1,20)=1.00$, $P>0.05$, Repetition, $F(1,20)=1.87$, $P>0.05$, or a significant Object \times Repetition interaction, $F(1,20)=0.19$, $P>0.05$.

Only target stimuli required an overt behavioral response. The reaction times to possible (438 ms, S.E.M.=13 ms), and impossible (434, S.E.M.=13 ms) stimuli were not significantly different, $F(1,20)=1.29$, $P>0.05$.

3.1.2. ERP results

ERP waveforms to first and second presentations of possible non-targets at a representative electrode from each of the six ROIs are illustrated in the left panel of Fig. 2. The data have two important features. First, at frontal electrode sites the second presentations elicited less negative waveforms than the initial presentations in a time window from about 250 to 400 ms. Second, at parieto-

occipital electrode sites the second presentations elicited a less positive waveform than the initial presentations in a time window from about 300 to 600 ms. The left panel of Fig. 3 presents topographical maps of the frontally localized positive difference and the parietally localized negative difference between repeated and first presentations of possible objects.

As the frontal and parieto-occipital effects were reversed in polarity and temporally overlapping, separate 2-way (Laterality \times Repetition) repeated measures ANOVAs were conducted on the mean ERP amplitudes from the frontal and parieto-occipital ROIs. A time window from 250 to 400 ms was used for the frontal analysis and a time window of 300–600 ms was used for the parieto-occipital analysis.

At both frontal and parieto-occipital ROIs the main effect of Repetition was significant, $F_s(1,20)=11.84$, and 42.54, respectively, both $P_s<0.05$, but it did not interact with Laterality, $F_s(2,40)=0.33$, and 1.84, respectively, both $P_s>0.05$.

ERP waveforms to repeated and non-repeated impossible non-targets at a representative electrode from each of the six ROIs are illustrated in the right panel of Fig. 2. The pattern of data was basically the same as that obtained for the possible non-targets. At frontal electrode sites the second presentations elicited less negative waveforms than the initial presentations, however, this effect was shorter in duration than that for the possible objects as it was present only between 250 and 350 ms. At parieto-occipital electrode sites the second presentations elicited less positive waveforms than the initial presentations in a time window from about 300 to 600 ms. The right panel of Fig. 3 presents topographical maps of the frontally localized positive difference and the parietally localized negative difference between second and first presentations of impossible objects.

Separate 2-way (Laterality \times Repetition) repeated measures ANOVAs were conducted on the mean ERP amplitudes for the frontal and parieto-occipital ROIs. A time window from 250 to 350 ms was used for the frontal analysis and a time window of 300–600 ms was used for the parieto-occipital analysis.

At frontal and parieto-occipital electrode sites the main effect of Repetition was significant, $F_s(1,20)=7.09$, and 52.18, respectively, both $P_s<0.05$, but it did not interact with Laterality, $F_s(2,40)=0.17$, and 1.43, respectively, both $P_s>0.05$.

Table 1

Group mean proportion correct for target items and for the first and second presentations of non-target items in Experiments 1 and 2 (S.E.M.)

	Target		Non-target			
	Possible	Impossible	Possible		Impossible	
			1st	2nd	1st	2nd
Exp. 1	1.000	0.997 (0.002)	0.997 (0.001)	0.998 (0.001)	0.998 (0.001)	1.000
Exp. 2	0.998 (0.002)	1.000	0.993 (0.002)	0.998 (0.001)	0.997 (0.002)	0.994 (0.004)

Difference Maps: 2nd - 1st Presentation

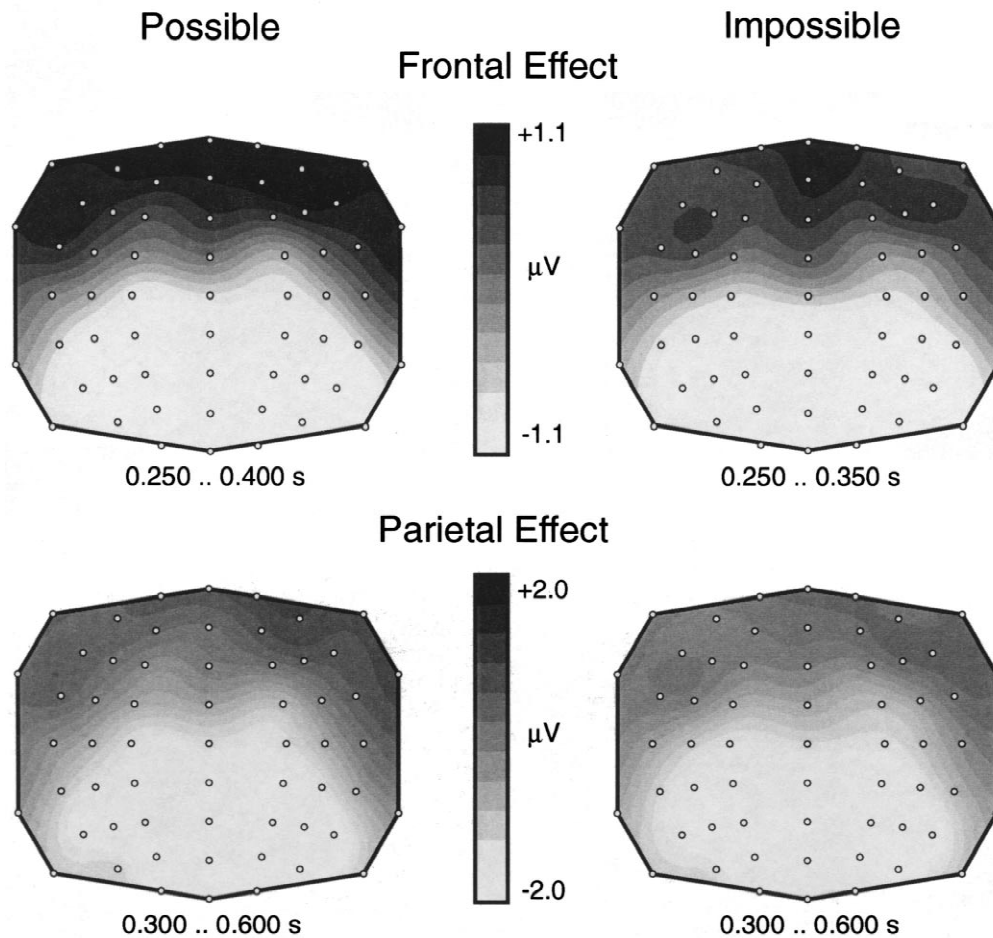


Fig. 3. Topographic maps of the ERP differences between second and first presentation of possible geometric figures (left side), and impossible geometric figures (right side). The top panels illustrate the frontal effect and the bottom panels the parietal effect. Note that the scaling of the topographical maps was adjusted to the magnitude of the effects.

3.2. Experiment 2

3.2.1. Behavioral performance

The group mean proportion of correctly identified stimuli, presented in Table 1, indicates that, as in Experiment 1, performance was excellent. On average, participants made fewer than 1% false alarms to possible and impossible objects on both first and second presentation and more than 99% of targets of both types were identified correctly. A 2-way ANOVA was conducted on the proportion correct responses to non-target items with Object Type (Possible, Impossible) and Repetition (1st and 2nd presentation) serving as repeated measures factors. For the non-target objects there was no significant effect of Object Type or Repetition, both $F_s(1,18) < 1.0$, but the Object \times Repetition interaction was significant, $F(1,18) = 5.70$, $P < 0.05$. Separate analyses for the Possible and Impossible objects indicated that the main effect of Repetition was not

significant for either Object Type, $F_s(1,18) = 3.08$ and 1.31 , respectively, both $P_s > 0.05$.

As in Experiment 1, only target stimuli required an overt behavioral response. The reaction times to possible (404 ms, S.E.M. = 13), and impossible (400 ms, S.E.M. = 14) target stimuli were not significantly different, $F(1,17) = 1.01$, $P > 0.05$. Note that the averages are for 18 of the 19 participants because reaction times were unavailable for one participant.

3.2.2. ERP results

ERP waveforms to first and second presentations of possible non-targets at a representative electrode from each of the six ROIs are illustrated in the left panel of Fig. 4. The data for the everyday objects are similar to those obtained for the possible 3-D geometric objects in Experiment 1. At frontal electrode sites the repeated items elicited less negative waveforms than the initial presentations in a time window from about 250 to 400 ms and at

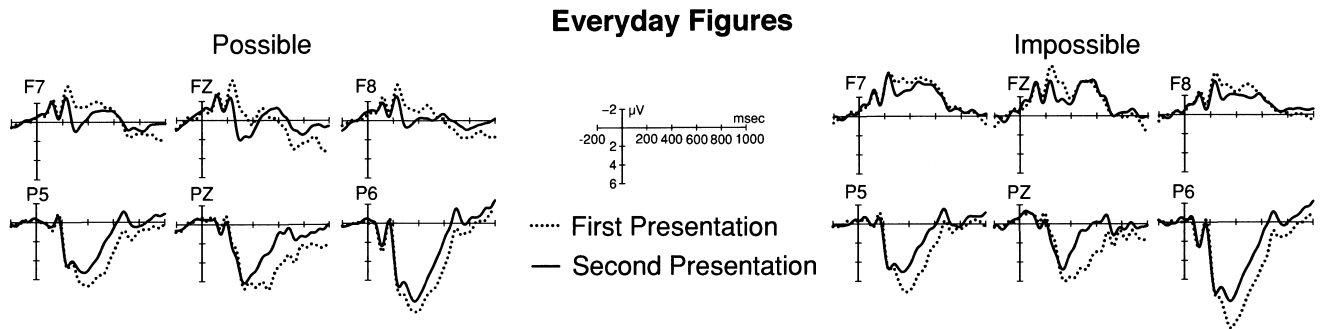


Fig. 4. ERP waveforms, averaged across subjects, elicited by the first and second presentations of possible (left side) and impossible (right side) Snodgrass figures. Waveforms are plotted for one electrode from each of the six ROIs. Time is on the x-axis (ms) and voltage is on the y-axis (uV, positive down). Only correct trials were included in the averages.

parieto-occipital electrode sites the repeated items elicited less positive waveforms than the initial presentations in a time window from about 300 to 600 ms. The left panel of Fig. 5 presents topographical maps of the frontally localized positive difference and the parietally localized nega-

tive difference between repeated and first presentations of possible objects.

Separate 2-way (Laterality×Repetition) repeated measures ANOVAs were conducted on the mean ERP amplitudes from the frontal and parieto-occipital ROIs. A

Difference Maps: 2nd - 1st Presentation

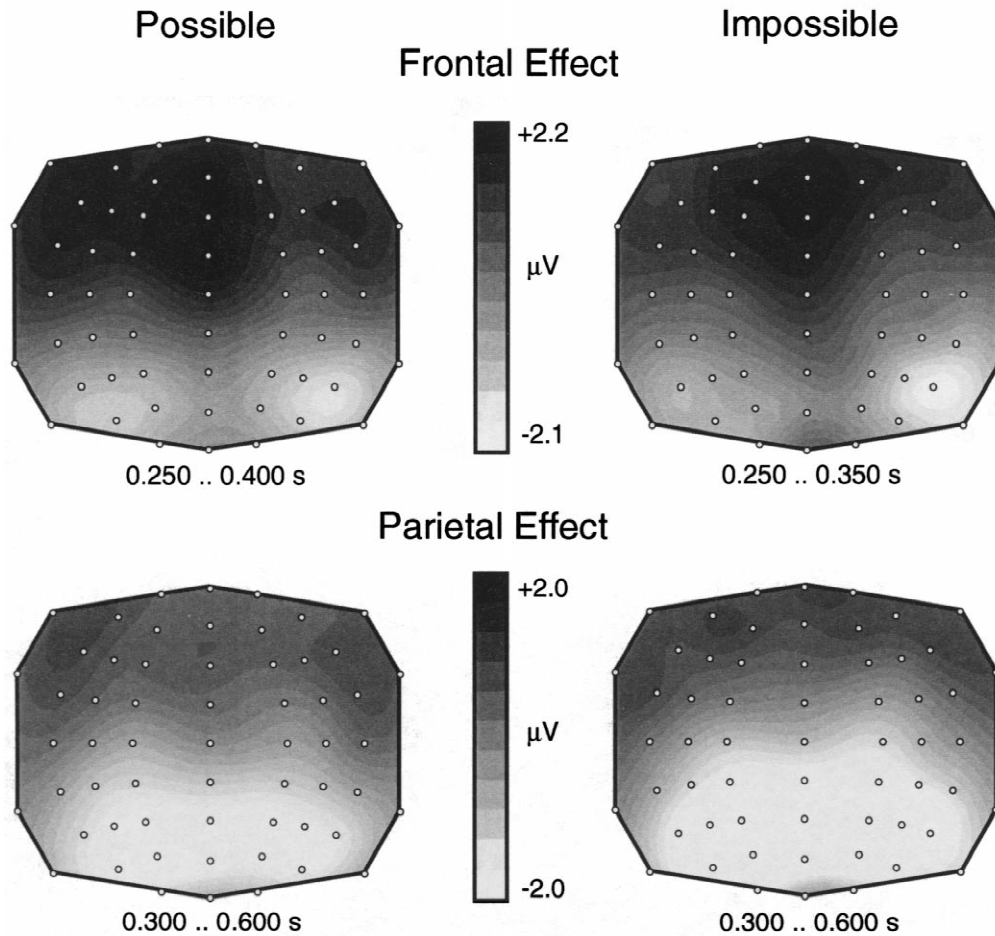


Fig. 5. Topographic maps of the ERP differences between second and first presentation of possible Snodgrass figures (left side), and impossible Snodgrass figures (right side). The top panels illustrate the frontal effect and the bottom panels the parietal effect. Note that the scaling of the topographical maps was adjusted to the magnitude of the effects.

time window from 250 to 400 ms was used for the analysis of frontal ROIs and a time window of 300–600 ms was used for the analysis of parieto-occipital ROIs.

At frontal electrode sites the main effect of Repetition was significant, $F(1,18)=16.56$, $P<0.05$, as was the Repetition \times Laterality interaction, $F(2,36)=7.97$, $P<0.05$. The simple main effect of Repetition was examined separately at each level of Laterality. The effect of Repetition was significant at all three ROIs, $F_s(1,18)=19.36$, 13.93, 13.60, for left, medial, and right ROIs respectively, $P_s<0.05$. The significant interaction, combined with voltage differences between second and first presentations of 1.11, 1.99, and 0.89 μ V for left, medial, and right ROIs respectively, indicates the frontal repetition effect had a left to medial focus.

At parieto-occipital electrode sites the main effect of Repetition was significant but the Repetition \times Laterality interaction was not, $F(1,18)=16.57$, $P<0.05$, and $F(2,40)<1.0$, respectively.

ERP waveforms to first and second presentations of impossible non-targets at a representative electrode from each of the six ROIs are illustrated in the right panel of Fig. 4. The data pattern is basically the same as that obtained for the possible non-targets. At frontal electrode sites the second presentations elicited less negative waveforms than the initial presentations. As for the impossible objects in Experiment 1, the effect was restricted to a smaller time window (i.e., 250–350 ms). At parieto-occipital electrode sites the second presentations elicited a less positive waveform than the initial presentations in a time window from about 300 to 600 ms. Separate 2-way (Laterality \times Repetition) repeated measures ANOVAs were conducted on the mean ERP amplitudes from the frontal and parieto-occipital ROIs. A time window from 250 to 350 ms was used for the frontal analysis and a time window of 300–600 ms was used for the parieto-occipital analysis. The right panel of Fig. 5 presents topographical maps of the frontally localized positive difference and the parietally localized negative difference between repeated and first presentations of impossible objects.

At frontal electrode sites the main effect of Repetition was significant, $F(1,18)=6.58$, $P<0.05$, and the Repetition \times Laterality interaction approached significance, and $F(2,36)=3.26$, $P=0.06$. Based on this marginally significant interaction, the simple main effects of Repetition were examined at each level of laterality. The effect of Repetition was significant at all three ROIs, $F_s(1,18)=4.79$, 7.35, and 6.38, for left, medial, and right ROIs respectively, $P_s<0.05$. The marginally significant interaction, combined with voltage differences between second and first presentations of 0.83, 1.22 and 0.76 μ V for left, medial, and right ROIs respectively, indicates the frontal repetition effect had a medial focus.

At parieto-occipital electrode sites the main effect of Repetition was significant but the Repetition \times Later-

ality interaction was not, $F(1,18)=20.07$, $P<0.05$, and $F(2,36)<1.0$, respectively.

4. Discussion

The ease of the task is demonstrated by the high correct detection rate for targets and the low false alarm rate to non-targets in both experiments. Equivalent false alarm rates to possible and impossible non-standards indicate that both object types were equally easy to distinguish from targets.

In Experiment 1, the ERP repetition effect was highly similar for possible and impossible geometric objects. At frontal electrode sites, waveforms to both object types were negative going relative to baseline and waveforms elicited by second presentations were less negative than those elicited by initial presentations. At more parietal electrode sites, waveforms to both object types were positive going relative to reference and the second presentations elicited less positive waveforms than the initial presentations. As the frontal and parietal effects obtained here had different onset latencies and temporal durations, it is clear that the neural generators for both effects were at least partially, if not entirely, unique. In addition, it is conceivable that both the exact onset of the parietal effect and the exact offset of the frontal effect were concealed by their overlap in time.

Interestingly, Rugg et al. [50] did not obtain an early frontal effect of repetition for possible geometric objects, although they did find a late frontal effect not observed here. The substantially faster average response times (a difference of 800 ms) and higher accuracy rates (a difference of 43%) in the present study indicate that the discrimination between the everyday target stimuli and the geometric non-target stimuli used here was easier than the discrimination between possible (non-targets) and impossible (targets) geometric objects in the Rugg et al. study. If the frontal effect is related to the target discrimination process, then a more difficult task requiring a longer decision time might fail to elicit the same ERP response. Consequently, the difference in tasks between the two experiments may account for the differences in ERP repetition effects.

More important, however, is that the the parietal ERP repetition effect observed here for both possible and impossible 3-D objects was highly similar in morphology, polarity, and topography to that observed by Rugg et al. [50] for possible 3-D objects, although its onset was about 100 ms later. Given that reaction times were faster in the present experiment, it is not clear why the parietal effect had a slightly later onset. As mentioned earlier, one possibility is that the temporal overlap with the frontally focused increase in positivity concealed the onset of the parietally focused decrease in positivity. In any case, Experiment 1 replicated the finding of a polarity reversed

immediate repetition effect for possible geometric objects [50] and extended the effect to include impossible geometric objects. Interestingly, Penney et al. [38] failed to obtain any effect of repetition on ERPs elicited by impossible geometric objects in an implicit memory (object decision) task, even though repeated possible geometric objects elicited a repetition effect consisting of an increased positivity to repeated stimuli over parietal-occipital electrode sites. The absence of a repetition effect for impossible objects was interpreted as due to the lack of a unitized code [46,49,50] for the geometrically impossible objects. In that study, however, there was a delay of approximately 20 min as well as 112 intervening stimuli, on average, between the initial stimulus exposure in the incidental encoding phase and the second presentation in the test phase. In addition, the stimulus classification required in the encoding phase was different from that required in the test phase. The absence of a repetition effect for impossible objects and the more typical increase in positivity for repeated possible objects obtained in that study, in combination with the repetition effects obtained for both object types in the present study, suggests that the presence of a delay and/or intervening items between first and second presentation as well as the specific demands of the experimental task are important determinants of the brain response. We return to this point later in the discussion.

In general, the ERP effects obtained with the everyday objects in Experiment 2 were the same as those obtained in Experiment 1, further extending the parietal reversed polarity ERP repetition effect to include line drawings of possible and impossible everyday objects. One important difference between the results of the two experiments, however, is that the frontal effect for the possible everyday objects had a left to medial focus and the impossible figures showed a similar marginally significant lateralization, whereas there was no such lateralization effect for the 3-D geometric objects. To confirm this apparent between-experiment laterality difference, separate ANOVAs for the possible and impossible objects were conducted on the rescaled difference waves (2nd minus 1st presentation) from Experiments 1 and 2. There was a significant Experiment \times Laterality interaction for the possible objects, $F(2,74)=3.17$, $P<0.05$, but not for the impossible objects. Although the neural tissue responsible for an ERP effect does not necessarily lie under the recording site, a left medial focus is consistent with brain imaging studies showing left-hemisphere activation during object naming [8,28,65] and also with studies suggesting that parts of the left frontal cortex are recruited during retrieval of lexical and semantic information [16,64]. This lateralization pattern suggests that access of lexical or semantic memory took place and was part of the target categorization process. As a consequence, it is plausible that, as proposed by Bentin and McCarthy [3], the frontal effect partially reflected fluency based on lexical/semantic access and the

reduced need for this access when the item was immediately repeated. Stimulus categorization was easier for recently presented items and this decrease in difficulty was reflected in a positive and frontally distributed ERP difference. According to Bentin and McCarthy, in categorical classification tasks, such as lexical decision and familiar–unfamiliar face discrimination, the need for stimulus analysis processes such as lexical/semantic access is reduced or eliminated and the decision process speeded because subjects are able to access an episodic memory representation of their previous classification of the stimulus. However, consideration of the results of Experiments 1 and 2 indicates that processes in addition to facilitation of semantic memory access contributed to the frontal effects obtained here. Possible and impossible geometric objects elicited similar frontal effects, although non-lateralized, to those elicited by the everyday objects even though it is unlikely that the geometric objects were represented in semantic memory. It is plausible that the frontal effect was composed of contributions from facilitated access to several different neural codes, e.g., access to an episodic representation of the immediately preceding classification of the stimulus, and lexical-semantic codes in the case of the everyday objects. In addition, it is possible that an image-based code was involved for both object types. Evidence that early ERP potentials over frontal electrode sites may reflect memory processes dependent on image-based rather than linguistic codes comes from a variety of paradigms. For example, Ganis et al. [17] reported that pictures presented at the end of sentences elicited an N400-like component that was significantly more frontally distributed than that for words. Furthermore, several studies requiring semantic relatedness judgments between sequentially presented line drawings or photographs showed an anteriorly distributed early negativity, with a peak at about 300 ms, that was larger for unrelated than for related pictures [2,20,29]. Finally, several studies of explicit memory for visual objects reported a reduction in an anterior N400-like component to old stimuli [31,32,38].

Moreover, a facilitation of processing interpretation is also suggested by the characterization of the ERP response elicited by second presentations as a reduction in neural activity relative to first presentations, i.e., the waveforms to second presentations were less negative at frontal sites and less positive at parietal sites. Indeed, this interpretation is also consistent with a number of neuroimaging studies of perceptual priming that show reductions in blood flow dependent measures of brain activity over posterior cortical sites when stimuli are repeated (e.g. [9,10,56], see [51] for review). In addition, neuroimaging studies of conceptual (semantic) priming show reduced activity to repeated presentations of words and pictures in the left inferior pre-frontal cortex (e.g. [16,62]), suggesting that this region is involved in the retrieval of semantic information from memory. Decreased neuronal activity is often taken to

indicate that stimulus analysis requires less computation when the item is repeated.

The neuronal basis for these ERP, PET, and fMRI effects is suggested by single unit recording studies in macaque monkeys. This work has shown that there are neurons in inferotemporal, and pre-frontal cortices, termed suppression cells, that reduce their firing rate when visual stimuli are repeated [13,33]. Consequently, it is plausible that the ERP difference between initial and repeated presentation in the present study was related to reduced activity of a human homolog of these suppression cells. That is, assuming that a reduction in firing rate occurs as a consequence of a decrease in excitatory post synaptic potentials or an increase in inhibitory post synaptic potentials, events that the scalp recorded ERP is sensitive to. One problem with this putative suppression cell explanation of the results from our repetition task relates to the latency of the parietal effect onset. Single unit studies in macaques using highly trained stimuli showed that suppression cells changed their firing rate beginning at about 80 ms after stimulus onset [13]. In the case of novel stimuli, the firing rate change occurred about 150–170 ms after stimulus onset [13]. In both cases, the latencies of the effects obtained in macaques were much earlier than the scalp recorded parietal ERP differences recorded here (onset of frontal effects at 250 ms and parietal effects at 300 ms). This does not, however, rule out that the effects were mediated by the same types of cells. Given that detectable differences at the scalp require synchronous activation of thousands of neurons [19], perhaps relatively large numbers of neurons were not simultaneously active until somewhat after the initial onset of unit firing in response to the stimulus. Alternatively, the present ERP results could reflect more downstream consequences of changes in the activity of suppression cells.

Independent of the underlying physiological mechanism, however, the question of what a reduction in neural activity means in terms of psychological function remains. Although the parietally focused reduced positivity to repeated stimuli appears consistent with neuro-imaging studies of priming that showed reduced blood flow dependent measures of neural activity to repeated stimuli [9,10,51,56], the typical ERP repetition effect, as described above, consists of increased positivity to repeated items. Perhaps the most obvious potential explanation, mentioned in the Introduction, is that the present reversal of the typical repetition effect was merely a consequence of the particular class of stimuli used. Conceivably, the neural tissue responsive to this class of visual stimuli, line drawings of geometric objects, is oriented differently from that underlying the more typical repetition effect. However, the parietal repetition effect for everyday objects was equivalent to that obtained for the novel geometric objects. Clearly, the polarity reversal was not a consequence of using novel geometric stimuli that did not have pre-existing semantic and/or canonical visuo-spatial representations in memory.

An alternative possibility is that the ERP difference between the second and the first presentation of an object reflected the availability of a newly-formed object representation that was short lasting and subject to interference from intervening stimuli (i.e., a token; [22,27,58]). Viggiano and Kutas [61], for example, required subjects to identify Snodgrass figures [55] that were presented at each of six levels of fragmentation in decreasing order, with the final figure being the complete version. They obtained an ERP difference between the overt identification fragmentation level and the first post-identification fragmentation level. At the post-identification stage, a late positivity emerged that had a sharper slope of onset, an earlier peak and a shorter duration than at identification — in effect, the waveform at the post-identification level was less positive than that obtained at the identification level. They suggested the reduction in positivity may have reflected the availability of newly formed representations in memory. This interpretation is further corroborated by Van Petten and colleagues [59], who found that repeated words in text elicited smaller late positive waves than new words. They argued that when reading a text the referent does not need to be newly retrieved from a long term store and that natural repetition of words in discourse invokes less extensive retrieval than new words because old words are part of an active mental representation. In a similar vein, the stimuli in the present study may have been temporarily maintained as visuo-spatial tokens with the consequence that there was less neural activity when those stimuli were repeated.

Moreover, a recent fMRI study by Jiang et al. [23] showed reductions, primarily in the extrastriate visual cortex, to non-target repeated faces in a working memory task. The authors claimed that this reduction may reflect a process that temporarily tags a familiar stimulus so that it can be processed more efficiently when encountered again within the context of the currently active working memory search. This finding raises the interesting question of whether priming and working memory processes share some common neuronal mechanisms and, importantly, whether the reversed polarity parietal ERP effect reported here was due to the immediate repetition of the stimulus. Indeed, it is true that most ERP repetition studies, whether of recognition memory or task irrelevant stimulus repetition, used substantial lags between initial and repeated presentations (e.g. [4–7]). Perhaps tasks incorporating a long lag between stimulus repetitions tap into processes that are very distinct from those accessed when a representation of the stimulus may still be active in a short term memory buffer. A simple repetition lag account, however, is not consistent with the available evidence in the literature. For example, there are a number of studies that used a lag of zero items between repetitions and still found the typical late positive component (e.g. [3,5,31,32]). In addition, a number of ERP studies of working memory that used an S1–S2 paradigm, meaning that on old trials items were immediately repeated, also found increased positivity

to old items [31,32]. Instead, it is probable that the polarity of the repetition effect depends on some combination of the task demands and the delay between initial and repeated presentations.

Nevertheless, these possibilities suggest a number of avenues for further research. For example, it is clearly important to determine the effects of the duration of the interstimulus interval and the presence of intervening stimuli on the repetition effect elicited by these stimuli in both a target detection task and in an explicit recognition task using the same stimulus stream. If the parietal effect is due to a representational token that is short lasting and susceptible to interference, then a lag between repeated stimuli and/or explicit memory demands may remove/reverse the effect. Furthermore, it is important to determine if the frontal and parietal effects depend on presenting the physically same stimulus on the initial and repeated trial or if a stimulus that has the same semantic content still modulates the waveforms in the same way.

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References

- [1] R.D. Badgaiyan, D.L. Schacter, N.M. Alpert, Auditory priming within and across modalities: Evidence from position emission tomography, *J. Cognit. Neurosci.* 11 (1999) 337–348.
- [2] S.E. Barrett, M.D. Rugg, Event-related potentials and the semantic matching of pictures, *Brain Cognit.* 14 (1990) 201–212.
- [3] S. Bentin, G. McCarthy, The effects of immediate stimulus repetition on reaction time and event-related potentials in tasks of different complexity, *J. Exp. Psychol.: Learn. Mem. Cognit.* 20 (1994) 130–149.
- [4] S. Bentin, M. Moscovitch, I. Heth, Memory with and without awareness: performance and electrophysiological evidence of savings, *J. Exp. Psychol.: Learn. Mem. Cognit.* 18 (1992) 1270–1283.
- [5] S. Bentin, B. Peled, The contribution of task-related factors to ERP repetition effects at short and long lags, *Mem. Cognit.* 18 (1990) 359–366.
- [6] M. Besson, M. Kutas, The many facets of repetition: a cued-recall and event-related potential analysis of repeating words in same versus different sentence contexts, *J. Exp. Psychol.: Learn. Mem. Cognit.* 19 (1993) 1115–1133.
- [7] M. Besson, M. Kutas, C. Van Petten, An event-related potential (ERP) analysis of semantic congruity and repetition effects in sentences, *J. Cognit. Neurosci.* 4 (1992) 132–149.
- [8] S.Y. Bookheimer, T.A. Zeffiro, T. Blaxton, W. Gaillard, W. Theodore, Regional cerebral blood flow during object naming and word reading, *Hum. Brain Mapp.* 3 (1995) 93–106.
- [9] R.L. Buckner, S.E. Petersen, J.G. Ojemann, F.M. Miezin, L.R. Squire, M.E. Raichle, Functional anatomical studies of explicit and implicit memory retrieval tasks, *J. Neurosci.* 15 (1995) 12–29.
- [10] R.L. Buckner, M.E. Raichle, F.M. Miezin, S.E. Petersen, Functional anatomic studies of memory retrieval for auditory words and visual pictures, *J. Neurosci.* 16 (1996) 6219–6235.
- [11] L.L. Chao, L. Nielsen-Bohman, R.T. Knight, Auditory event-related potentials dissociate early and late memory processes, *Electroencephalogr. Clin. Neurophysiol.* 96 (1995) 157–168.
- [12] Y.M. Cykowicz, D. Friedman, ERP recordings during a picture fragment completion task: effects of memory instructions, *Brain Res. Cognit. Brain Res.* 8 (1999) 271–288.
- [13] R. Desimone, E.K. Miller, L. Chelazzi, The interaction of neural systems for attention and memory, in: C. Koch, J.L. Davis (Eds.), *Large-Scale Neuronal Theories of the Brain*, Computational Neuroscience, MIT Press, Cambridge, MA, 1994, pp. 75–91.
- [14] M.C. Doyle, M.D. Rugg, Word repetition within- and across-visual fields: an event-related potential study, *Neuropsychologia* 36 (1998) 1403–1415.
- [15] D. Friedman, Cognitive event-related potential components during continuous recognition memory for pictures, *Psychophysiology* 27 (1990) 136–148.
- [16] J.D.E. Gabrieli, J.E. Desmond, J.B. Demb, A.D. Wagner, M.V. Stone, C.J. Vaidya, G.H. Glover, Functional magnetic resonance imaging of semantic memory processes in the frontal lobes, *Psychol. Sci.* 7 (1996) 279–283.
- [17] G. Ganis, M. Kutas, M. Sereno, The search for ‘Common Sense’: An electrophysiological study of the comprehension of words and pictures in reading, *J. Cognit. Neurosci.* 8 (1996) 89–106.
- [18] S. Greenhouse, S. Geisser, On methods in the analysis of profile data, *Psychometrika* 24 (1959) 95–112.
- [19] M. Hämäläinen, R. Hari, R.J. Ilmoniemi, J. Knuutila, O.V. Lounasmaa, Magnetoencephalography — theory, instrumentation, and applications to noninvasive studies of the working human brain, *Rev. Mod. Phys.* 65 (1993) 413–497.
- [20] P.J. Holcomb, W.B. McPherson, Event-related brain potentials reflect semantic processing in an object decision task, *Brain Cognit.* 24 (1994) 259–276.
- [21] R.W. Homan, J. Herman, P. Purdy, Cerebral location of the international 10–20 system electrode placement, *Electroencephalogr. Clin. Neurophysiol.* 66 (1987) 376–382.
- [22] A. Ishai, D. Sagi, Common mechanisms of visual imagery and perception, *Science* 268 (1995) 1772–1774.
- [23] Y. Jiang, J.V. Haxby, A. Martin, L.G. Ungerleider, R. Parasuraman, Complementary neural mechanisms for tracking items in human working memory, *Science* 287 (2000) 643–646.
- [24] R. Johnson, K. Kreiter, B. Russo, J. Zhu, A spatio-temporal analysis of recognition-related event-related brain potentials, *Int. J. Psychophysiol.* 29 (1998) 83–104.
- [25] C.A. Joyce, K.A. Paller, H.K. McIsaac, M. Kutas, Memory changes with normal aging: Behavioral and electrophysiological measures, *Psychophysiology* 35 (1998) 669–678.
- [26] V.A. Kazmerski, D. Friedman, Effect of multiple presentations of words on event-related potential and reaction time repetition effects in Alzheimer’s patients and young and older controls, *Neuropsych. Neuropsychol. Behav. Neurol.* 10 (1997) 32–47.
- [27] B.J. Knowlton, L.R. Squire, The learning of natural categories: Parallel memory systems for item memory and perceptual learning, *Science* 262 (1993) 1747–1749.
- [28] A. Martin, C.L. Wiggs, L.G. Ungerleider, J.V. Haxby, Neural correlates of category specific knowledge, *Nature* 379 (1996) 649–652.
- [29] W.B. McPherson, P.J. Holcomb, An electrophysiological investigation of semantic priming with pictures of real objects, *Psychophysiology* 36 (1999) 53–65.
- [30] A. Mecklinger, *Interfacing mind and brain: A neurocognitive model of recognition memory*, *Psychophysiology* (in press).
- [31] A. Mecklinger, On the modularity of recognition memory for object form and spatial location: a topographic ERP analysis, *Neuropsychologia* 36 (1998) 441–460.
- [32] A. Mecklinger, R.M. Meinshausen, Recognition memory for object form and spatial location: An event-related potential study, *Mem. Cognit.* 26 (1998) 1068–1088.
- [33] E.K. Miller, R. Desimone, Parallel neuronal mechanisms for short-term memory, *Science* 263 (1994) 520–522.

- [34] P.F. Mitchell, S. Andrews, P.B. Ward, An event-related potential study of semantic congruity and repetition in a sentence-reading task: effects of context change, *Psychophysiology* 30 (1993) 496–509.
- [35] K.A. Paller, M. Gross, Brain potentials associated with perceptual priming vs. explicit remembering during the repetition of visual word form, *Neuropsychologia* 36 (1998) 559–571.
- [36] K.A. Paller, M. Kutas, Brain potentials during memory retrieval provide neuropsychological support for the distinction between conscious recollection and priming, *J. Cognit. Neurosci.* 4 (1992) 375–391.
- [37] K.A. Paller, M. Kutas, H.K. McIsaac, Monitoring conscious recollection via the electrical activity of the brain, *Psychol. Sci.* 6 (1995) 107–111.
- [38] T.B. Penney, A. Mecklinger, H.J. Hilton, L.A. Cooper, Priming and Recognition of novel 3-D objects: Guidance from event-related potentials, *Cognit. Sci. Quarterly* 1 (2000) 69–92.
- [39] F. Perrin, J. Pernier, O. Bertrand, J. Echallier, Spherical splines for scalp potential and current density mapping, *Electroencephalogr. Clin. Neurophysiol.* 72 (1989) 184–187.
- [40] C. Ranganath, K.A. Paller, Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual detail, *Neuron* 22 (1999) 605–613.
- [41] P.J. Reber, C.E.L. Stark, L.R. Squire, Contrasting cortical activity associated with category memory and recognition memory, *Learn. Mem.* 5 (1998) 420–428.
- [42] M.D. Rugg, ERP studies of memory, in: M.D. Rugg, M.G.H. Coles (Eds.), *Electrophysiology of Mind*, Oxford University Press, Oxford, UK, 1995, pp. 132–170.
- [43] M.D. Rugg, Event-related brain potentials dissociate repetition effects of high- and low-frequency words, *Mem. Cognit.* 18 (1990) 367–379.
- [44] M.D. Rugg, Dissociation of semantic priming, word and non-word repetition effects by event-related potentials, *Q. J. Exp. Psychol.* 39A (1987) 123–148.
- [45] M.D. Rugg, The effects of semantic priming and word repetition on event-related potentials, *Psychophysiology* 22 (1985) 642–647.
- [46] M.D. Rugg, M.C. Doyle, Event-related potentials and stimulus repetition in indirect and direct tests of memory, in: H. Heinze, T. Munte, G.R. Mangun (Eds.), *Cognitive Electrophysiology*, Birkhauser Boston, Cambridge, MA, 1994, pp. 124–148.
- [47] M.D. Rugg, M.C. Doyle, Event-related potentials and recognition memory for low- and high-frequency words, *J. Cognit. Neurosci.* 4 (1992) 69–79.
- [48] M.D. Rugg, R.E. Mark, P. Walla, A.M. Schloerscheidt, C.S. Birch, K. Allan, Dissociation of the neural correlates of implicit and explicit memory, *Nature* 392 (1998) 595–598.
- [49] M.D. Rugg, M.E. Nagy, Lexical contribution to non-word-repetition effects: evidence from event-related potentials, *Mem. Cognit.* 15 (1987) 473–481.
- [50] M.D. Rugg, M. Soardi, M.C. Doyle, Modulation of event-related potentials by the repetition of drawings of novel objects, *Brain Res. Cognit. Brain Res.* 3 (1995) 17–24.
- [51] D.L. Schacter, R.L. Buckner, Priming and the brain, *Neuron* 20 (1998) 185–195.
- [52] D.L. Schacter, L.A. Cooper, S.M. Delaney, Implicit memory for unfamiliar objects depends on access to structural descriptions, *J. Exp. Psychol.: General* 119 (1990) 5–24.
- [53] D.M. Schnyer, J.J.B. Allen, K.I. Forster, Event-related brain potential examination of implicit memory processes: masked and unmasked repetition priming, *Neuropsychology* 11 (1997) 243–260.
- [54] M.E. Smith, K. Guster, Decomposition of recognition memory event-related potentials yields target, repetition, and retrieval effects, *Electroencephalogr. Clin. Neurophysiol.* 86 (1993) 335–343.
- [55] J.G. Snodgrass, M. Vanderwart, A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity, *J. Exp. Psychol.: Hum. Learn. Mem.* 6 (1980) 174–215.
- [56] L.R. Squire, J.G. Ojemann, F.M. Miezian, S.E. Petersen, T.O. Videen, M.E. Raichle, Activation of the hippocampus in normal humans: A functional anatomical study of memory, *Proc. Natl. Acad. Sci.* 89 (1992) 1837–1841.
- [57] D. Swick, R.T. Knight, Event-related potentials differentiate the effects of aging on word and nonword repetition in explicit and implicit memory tasks, *J. Exp. Psychol.: Learn. Mem. Cognit.* 23 (1997) 123–142.
- [58] A. Treisman, Perceiving and re-perceiving objects, *Am Psychol.* 47 (1992) 862–875.
- [59] C. Van Petten, M. Kutas, R. Kluender, M. Mitchener, H. McIsaac, Fractionating the word repetition effect with event-related potentials, *J. Cognit. Neurosci.* 3 (1991) 131–150.
- [60] C. Van Petten, A.J. Senkfor, Memory for words and novel visual patterns: Repetition, recognition, and encoding effects in the event-related potential, *Psychophysiology* 33 (1996) 491–506.
- [61] M.P. Viggiano, M. Kutas, The covert interplay between perception and memory: event related potential evidence, *Electroencephalogr. Clin. Neurophysiol.* 10 (1998) 435–439.
- [62] A.D. Wagner, J.E. Desmond, J.B. Demb, G.H. Glover, J.D.E. Gabrieli, Semantic repetition priming for verbal and pictorial knowledge: A functional MRI study of left inferior prefrontal cortex, *J. Cognit. Neurosci.* 9 (1997) 714–726.
- [63] C.L. Wiggs, A. Martin, Properties and mechanisms of perceptual priming, *Curr. Opin. Neurobiol.* 8 (1998) 233–277.
- [64] C.L. Wiggs, J. Weisberg, A. Martin, Neural correlates of semantic and episodic memory retrieval, *Neuropsychologia* 37 (1999) 103–118.
- [65] B.J. Zelkowitz, A.N. Herbster, R.D. Nebes, M.A. Mintun, J.T. Becker, An examination of regional cerebral blood flow during object naming tasks, *J. Int. Neuropsychol. Soc.* 4 (1998) 160–166.