

Controlling for interstimulus perceptual variance abolishes N170 face selectivity

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Establishing when and how the human brain differentiates between object categories is key to understanding visual cognition. Event-related potential (ERP) investigations have led to the consensus that faces selectively elicit a negative wave peaking 170 ms after presentation, the 'N170'. In such experiments, however, faces are nearly always presented from a full front view, whereas other stimuli are more perceptually variable, leading to uncontrolled interstimulus perceptual variance (ISPV). Here, we compared ERPs elicited by faces, cars and butterflies while—for the first time—controlling ISPV (low or high). Surprisingly, the N170 was sensitive, not to object category, but to ISPV. In addition, we found category effects independent of ISPV 70 ms earlier than has been generally reported. These results demonstrate early ERP category effects in the visual domain, call into question the face selectivity of the N170 and establish ISPV as a critical factor to control in experiments relying on multitrial averaging.

In the study of human cognition, one major endeavor is to identify the functional dissociations that reveal how the brain organizes conceptual knowledge. For instance, cognitive neuroscientists have attempted to characterize the neural substrates involved in categorizing objects in the environment. In pursuit of this goal, numerous ERP and, more recently, magnetoencephalography (MEG) studies have investigated the time course of category effects in visual object recognition. These have led to the observation that a specific electrical response systematically occurs for faces at a latency of 170 ms after stimulus onset, which is characterized by a vertex positive and bilateral temporal negative deflection^{1–3}. A consensus has now been reached regarding the face-specificity of the N170 (refs. 4–6) and its magnetic equivalent, the M170 (refs. 7,8), as no other stimulus category is reported to elicit negativities as pronounced as faces at 170 ms or to share the same scalp topography⁵. The sensitivity of the N170 to faces, however, is not necessarily interpreted as evidence for a face-specific modular system in the human brain, as modulation of the N170 by expertise is found for objects other than faces^{9,10}. Furthermore, it has been argued that low-level visual characteristics of the stimuli could account at least in part for some of the differences observed between categories of objects¹¹.

Because neuroimaging studies of visual face and object recognition generally use full front views of faces contrasted with pictures of other objects presented in a variety of sizes and spatial layouts, category contrasts typically involve implicit comparisons of low and high ISPV conditions (Fig. 1). Unfortunately, as the amount of ISPV involved is virtually never evaluated or reported (see ref. 5 for an exception), it is impossible to know whether differences between experimental conditions arise from categorical differences or whether they are merely driven by ISPV. We therefore formulated the hypothesis that the face

selectivity of the N170 might be an artifact driven by ISPV differences. To test this hypothesis, we manipulated ISPV as an experimental factor independently of object category: we compared the ERPs elicited by pictures of faces and cars, half of which were highly variable in position, orientation and size, and half of which were systematically centered, full front, and resized to fit in a predefined template (Fig. 2). If the N170 is genuinely face selective, its amplitude should be relatively insensitive to ISPV, but maximally sensitive to object category (Experiment 1). We then tested whether the effects of ISPV found in Experiment 1 could be due to differences in symmetry between high and low ISPV conditions by comparing ERPs elicited by side views of faces and butterflies, half of which had low ISPV and half of which had high ISPV (Experiment 2, Fig. 2). Another aspect of Experiment 2 is that the high ISPV stimuli were generated by manipulating the size, eccentricity and height/width ratio of the stimuli from the low ISPV condition. This enabled us to control for stimulus variance in the stimuli while holding object similarity from a psychological standpoint relatively constant. Finally, we tested whether the effects seen in Experiments 1 and 2 could be due to faces attracting attention more than other objects. We compared the ERPs elicited by pictures of blue and green overlapped faces and cars that were controlled for ISPV (Fig. 3), and instructed participants to detect repetition of images in one color only (Experiment 3). Here we expected differential attentional effects on P1 and N170 amplitude elicited by faces and potentially confounding ISPV modulations in Experiment 1 and 2 to be revealed.

RESULTS

Controlling ISPV cancels N170 face-selectivity

In Experiment 1, visual ERPs recorded in 28 participants displayed a characteristic P1-N1-P2 complex in all experimental conditions

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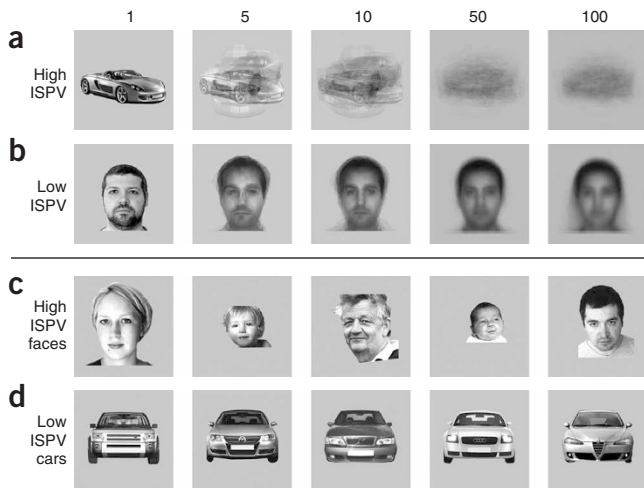


Figure 1 Visualizing interstimulus perceptual variance. (a) Progressive pixel-by-pixel averaging of pictures of cars typically used in experiments testing object categorization. (b) Progressive averaging of pictures of faces typically used in the same type of experiments. The number of stimuli used in each average is printed above each column. In the low ISPV condition, the stimulus category can still be identified in an average of 100 pictures, but that is not the case in the high ISPV condition. (c) Examples of faces varying in size, orientation and eccentricity belonging to the high ISPV condition in Experiment 1. (d) Examples of cars matched for size, orientation and eccentricity belonging to the low ISPV condition in Experiment 1.

(Fig. 4). Mean accuracy was $84.5 \pm 12.5\%$ and the rate of false alarms was $4.7 \pm 3.8\%$.

Repeated measures analysis of variance (ANOVA) on N170 amplitudes over ten parietooccipital electrodes showed a main effect of ISPV ($F_{1,27} = 24.39$, $P < 0.0001$), that the N170 was significantly greater in the low than in the high ISPV condition (Fig. 4a). Notably, object category (face or car) had no measurable effect on N170 peak amplitude ($F_{1,27} = 1.33$, $P > 0.1$; Fig. 4b). In addition, category and ISPV interacted ($F_{1,27} = 8.28$, $P < 0.01$); the difference between N170s in the low and high ISPV conditions for cars was greater than for faces (Fig. 4c). In spite of the interaction, however, post-hoc comparisons showed significant low versus high ISPV differences for both faces ($P < 0.01$) and cars ($P < 0.0001$). It is noteworthy that the contrast usually reported in the literature, low ISPV faces versus high ISPV cars, was significant ($P < 0.01$).

In contrast, analysis of P1 amplitudes produced a pattern of response that had originally been predicted for the N170 (Fig. 4c). There was a main effect of object category on P1 peak amplitude ($F_{1,27} = 13.57$, $P < 0.001$) showing that the P1 elicited by faces was significantly larger than the P1 elicited by cars, but notably, there was no effect of ISPV on P1 amplitude ($F_{1,27} = 0.18$, $P > 0.1$) and no interaction between the two factors ($F_{1,27} = 0.48$, $P > 0.1$).

To confirm the sensitivity of the N170 to ISPV and that of the P1 to object category, we used a temporal segmentation procedure (see Methods) to determine the pattern, number

and duration of topographic maps of scalp electrical activity (functional microstates). The segmentation procedure identified two distinct functional microstates in the P1 range, one for each object category, which we labeled P1f and P1c. By contrast, only one microstate was identified in the N170 range that differed on the basis of its intensity with respect to the level of ISPV, following the same dissociations found in the amplitude analyses (Fig. 5a).

We computed the degree to which maps P1f and P1c fit each individual map series in the 80–160-ms time window by measuring the amount of variance explained in every subject, and entering these values into a 2 (map) $\times 2$ (category) $\times 2$ (ISPV) repeated measures ANOVA (see Methods). Post-hoc statistical tests exploring a highly significant map \times category interaction ($F_{1,27} = 17.45$; $P < 0.001$) showed that map P1f accounted significantly more for individual ERPs elicited by faces than did map P1c ($P < 0.01$) and, conversely, that map P1c better accounted for individual ERPs elicited by cars than did P1f ($P < 0.05$; Fig. 5b).

The N170 had a similar topography for both object categories but appeared significantly earlier ($F_{1,27} = 28.14$; $P < 0.0001$) for faces (low ISPV: 166 ms, high ISPV: 170 ms) than for cars (low ISPV: 176 ms; high ISPV: 179 ms). Furthermore, we found a main effect of ISPV ($F_{1,27} = 28.14$; $P < 0.001$), that the intensity of the N170 topography, that is, the global field power, was greater for low ISPV (faces: $2.83 \mu\text{V}$, cars: $3.0 \mu\text{V}$) than for high ISPV (faces: $2.35 \mu\text{V}$; cars: $2.14 \mu\text{V}$; $F_{1,20} = 12.34$, $P < 0.01$).

Thus, faces and cars gave rise to distinct functional microstates in the P1 range, whereas maps in the N170 range were identical across these two categories, differing only in timing and intensity with respect to the level of ISPV.

ISPV effects are not driven by image symmetry

As in Experiment 1, ERPs elicited by side views of faces and butterflies (Fig. 2) in 27 participants displayed the characteristic P1-N1-P2 complex in the four conditions of Experiment 2 (Fig. 6). Mean accuracy was $83.2 \pm 9.7\%$ and the rate of false alarms was $5.9 \pm 4.7\%$.

Repeated measures ANOVAs performed on N1 amplitudes over ten parietooccipital electrodes showed a main effect of ISPV ($F_{1,26} = 60.04$, $P < 0.0001$), that the N170 was significantly greater in the low than in the high ISPV condition (Fig. 6a). Again, object

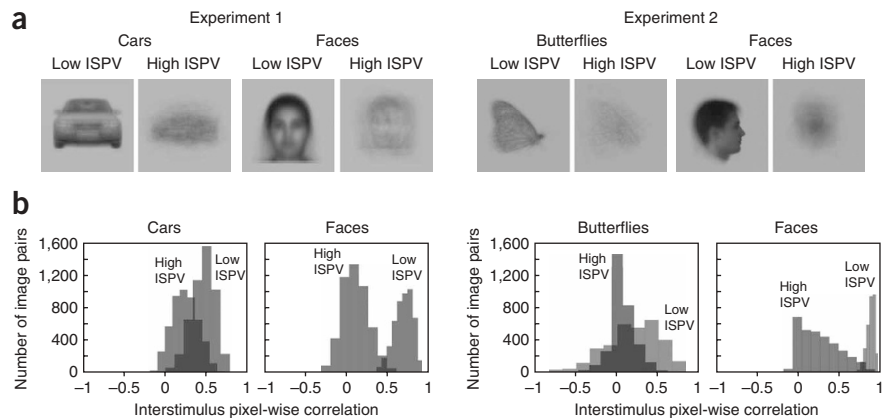


Figure 2 Visualization of ISPV in Experiment 1 (left) and 2 (right). (a) Pixel-by-pixel averages of the stimuli presented in each of the experimental conditions. (b) Histogram of pixel-wise correlation between stimuli in each category showing the distributions for the two levels of ISPV. These correlations provide a quantitative measure of overlap among images in each condition at the pixel-by-pixel level, but may not index information psychologically relevant for object recognition.

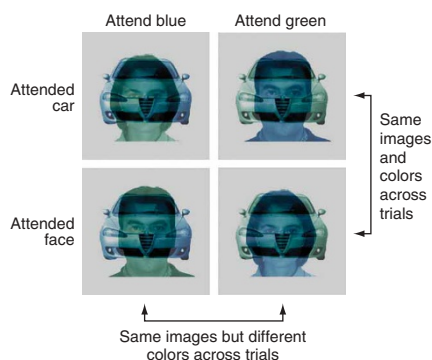


Figure 3 Design of Experiment 3. The same overlays of faces and cars were presented in the attend blue and attend green conditions. When grouping the trials based on the attended category (car/face) across the attend blue and attend green blocks, the same car was presented once in blue and once in green. Therefore, when we compared the attended car with the attended face conditions, the two stimulus pools were identical over the entire experiment.

category (face or butterfly) had no significant effect on N170 mean amplitude ($F_{1,26} = 2.84$, $P > 0.1$; **Fig. 6b**). Unlike in Experiment 1, category and ISPV did not interact ($F_{1,26} = 0.83$, $P > 0.1$).

Analysis of P1 amplitudes produced the same pattern of response seen in Experiment 1 (**Fig. 6c**). There was a main effect of object category on P1 amplitude ($F_{1,26} = 33.58$, $P < 0.0001$), showing that the P1 elicited by faces was significantly larger than the P1 elicited by butterflies and, notably, no effect of ISPV on P1 amplitude was found ($F_{1,26} = 1.36$, $P > 0.1$) and there was no interaction between the two factors ($F_{1,26} = 0.43$, $P > 0.1$).

We submitted the dataset obtained in Experiment 2 to the same temporal segmentation procedure used in Experiment 1. As before, the algorithm produced two distinct functional microstates in the P1 range, independently of ISPV, one for faces—labeled P1f—and one for butterflies—labeled P1b. Again, only one microstate was identified in the N170 range that only differed in intensity between low and high ISPV conditions. The statistical validity of maps P1f' and P1b was then tested by determining the amount of variance explained by each of the two maps in the ERP map series of each individual between 80 and 160 ms in the four conditions. The explained variance was entered into a 2 (map) \times 2 (category) \times 2 (ISPV) ANOVA. A significant interaction was found between category and map ($F_{1,26} = 58.16$; $P < 0.0001$) such that P1f' better explained individual face than butterfly map series (post-hoc LSD; $P < 0.0001$), whereas map P1b better explained

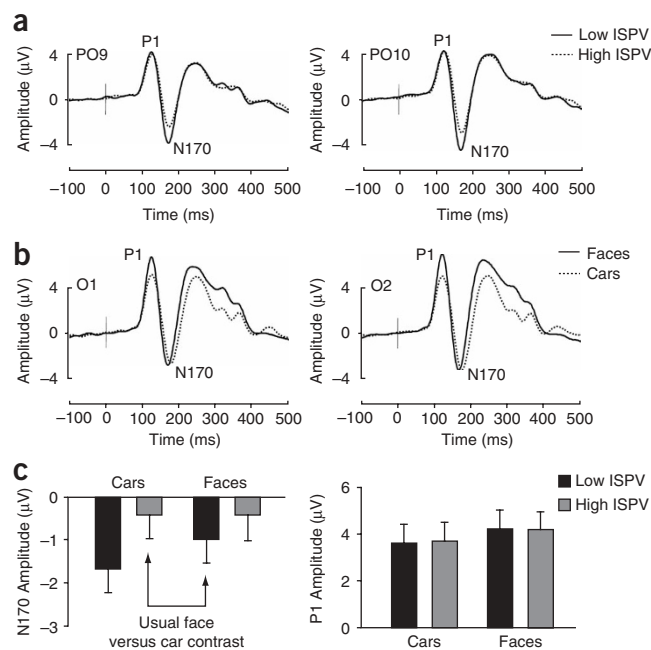


Figure 4 Event-related potential results from Experiment 1. (a) Main effect of ISPV at electrodes of maximal sensitivity (PO9 and PO10). (b) Main effect of object category at electrodes of maximal sensitivity (O1 and O2). (c) Mean amplitude of N170 and P1 peaks over the ten most posterior parietooccipital electrodes (see Methods). Error bars depict s.e.m.

butterfly than face map series (post-hoc LSD; $P < 0.001$). As in Experiment 1, the N170 had a similar topography for both object categories, but it was significantly more intense for low ISPV (faces: $3.03 \mu\text{V}$, butterflies: $2.89 \mu\text{V}$) than for high ISPV (faces: $2.7 \mu\text{V}$; butterflies: $2.48 \mu\text{V}$; $F_{1,26} = 15.58$, $P < 0.001$).

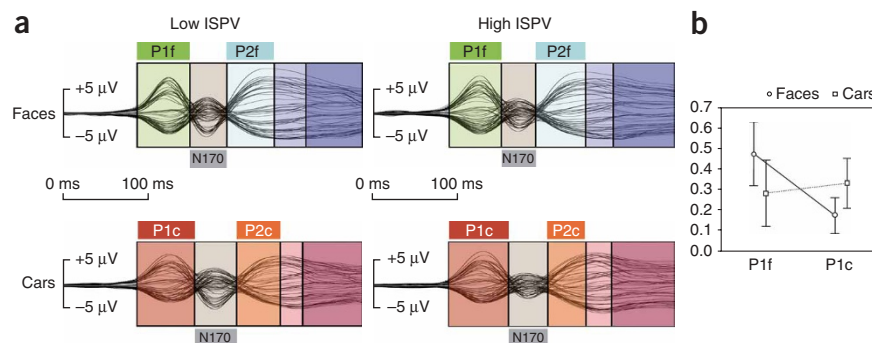
In sum, replicating the results of Experiment 1 using asymmetrical stimuli and a different nonface contrast category, faces and butterflies elicited distinct functional microstates in the P1 range, but maps in the N170 range were identical between the two categories, differing only in intensity with respect to the level of ISPV.

Category and ISPV effects are not confounded by attention

In Experiment 3, we presented participants with overlays of faces and cars in two colors (blue and green) and instructed them to press a button for picture repetitions in one of the two colors only (for example, the same blue object, ignoring green ones). Notably, we

Figure 5 Topographic segmentation analysis and amount of variance explained by maps P1f (faces) and P1c (cars) in the P1 range in Experiment 1.

(a) Five maps accounted for the four grand-average conditions between 80 and 250 ms. The P1 was best explained by two different maps, P1f and P1c, elicited by faces and cars, respectively. In the N170 range, low and high ISPV conditions elicited the same N170 map, irrespective of category, although differences in ISPV were accompanied by differences in overall potential. Other maps relate to higher order processes not discussed in this paper. However, the subsequent series of maps tended to abide by the object category divide rather than the ISPV divide. (b) The average amount of variance (max = 1) explained in the 80–160-ms time period by maps P1f and P1c in individual ERP map series is plotted for faces (circles) and cars (squares). Vertical bars depict 95% confidence intervals.



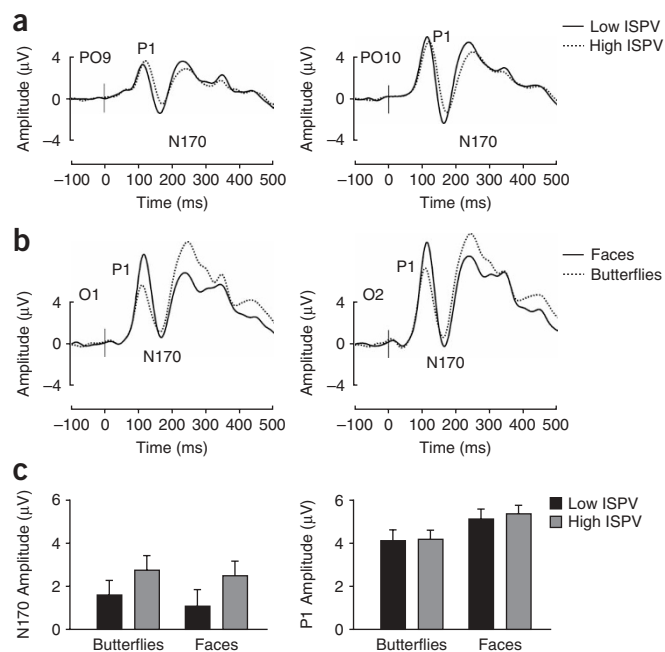


Figure 6 Event-related potential results from Experiment 2. (a) Main effect of ISPV at electrodes PO9 and PO10 for comparison with **Figure 4**. (b) Main effect of object category at electrodes of maximum sensitivity (O1 and O2). (c) Mean amplitude of N170 and P1 peaks over the ten most posterior parietooccipital electrodes (see Methods). Error bars depict s.e.m.

designed the experiment such that sorting trials by attended category (face or car) across the attend blue and attend green conditions would lead to comparing ERPs elicited by the exact same physical stimuli overall (**Fig. 3** and Methods). In other words, the attended face versus attended car comparison was, on average, free of perceptual differences.

Twenty of the 27 participants involved correctly detected more than half of the repetitions. In these 20 participants, the mean rate of correct detection was $72.5 \pm 13.7\%$ and the mean rate of false alarms was $7.7 \pm 5.1\%$. ERPs recorded in these participants showed the characteristic P1-N1-P2 complex in the four conditions of Experiment 3 (**Fig. 7**). Attended category irrespective of attended color failed to affect the amplitude of the P1 ($F_{1,19} = 0.78$, $P > 0.1$) or the N170 ($F_{1,19} = 0.18$, $P > 0.1$). There were also no latency differences in the P1 and N170 range. Significant differences between attended cars and faces appeared only after 300 ms. In sum, as found in previous studies^{12–14}, a direct manipulation of attention to stimulus category did not modulate the amplitude of the P1 and N170, and so attentional confounds are unlikely to explain the results of the previous two experiments.

DISCUSSION

This study was aimed at testing the robustness of the N170 ERP wave in relation to ISPV. Manipulating ISPV showed that the N170 is significantly affected by the low-level perceptual overlap between pictures presented in different trials and that, when ISPV is controlled, discrimination between cars and faces is not seen in the expected time range of 170 ms after stimulus onset, but 70 ms earlier. In addition, topographical analyses confirmed that functional microstates differ significantly as a function of category, but not of ISPV, in the P1 range, whereas topographies are identical in the N170 range, but differ in strength.

The previously unknown dissociation between category sensitivity in the P1 range and ISPV sensitivity in the N170 range found in

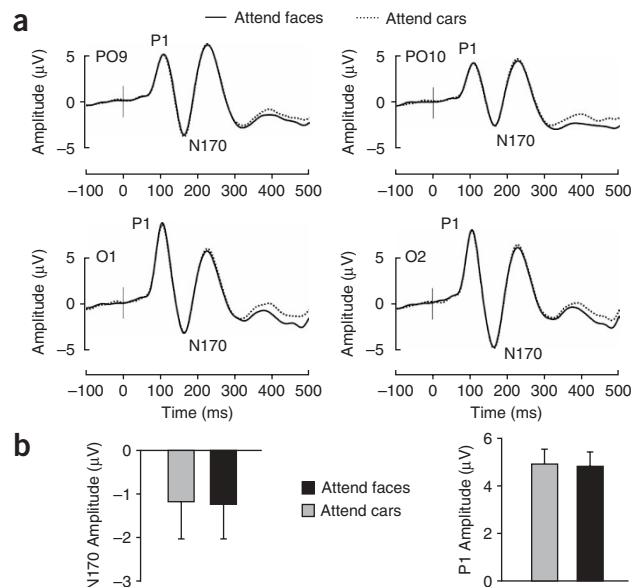


Figure 7 Event-related potential results from Experiment 3. (a) Main effect of attended category at electrodes PO9, PO10, O1 and O2 for comparison with **Figures 4** and **6**. (b) Mean amplitude of N170 and P1 peaks over the ten most posterior parietooccipital electrodes (see Methods). Error bars depict s.e.m. Note the perfect overlap of the waveforms until after 300 ms and that the stimuli were overall physically identical in the two conditions.

Experiment 1 was replicated in Experiment 2, which involved asymmetrical images (face profiles and side views of butterflies). This shows that ISPV effects on N170 amplitude are not confounded by differences in image symmetry between low and high ISPV conditions. Furthermore, in Experiment 2, the high ISPV stimuli were directly derived from the low ISPV stimuli by altering only size, eccentricity and proportions, but not symmetry and orientation. The N170 is therefore sensitive to ISPV even when the overall composition of the object is fundamentally the same in high and low ISPV conditions. Thus, the modulation of the N170 reported here is not entirely explainable by differences in perceptual similarity¹⁵.

On the other hand, the P1, a peak generally regarded as an index of lower level perceptual processing^{16–19}, was surprisingly unaffected by differences in ISPV, but was sensitive to object category in both Experiments 1 and 2. This should not be interpreted as evidence for absolute category selectivity because only three object categories were tested here. Indeed, faces, cars and butterflies differ in terms of overall composition and various perceptual properties such as outline, contrast, subparts and complexity, which were not manipulated here. It is therefore possible that the P1 still reflects perceptual differences between these objects; that is, that apparent category selectivity in this component is an emergent property arising from low perceptual invariants.

The results from Experiments 1 and 2 could not be explained by differences in task difficulty or cognitive strategy between experimental conditions because trials from every condition were randomly mixed throughout the experiments (Methods). One potential confound regarding P1 category sensitivity was that faces may have attracted more attention than other objects. By comparing the ERPs elicited by attended faces and cars in dual-color overlaps in Experiment 3, we ruled out possible modulation of P1 amplitude by early selective attention to faces. Indeed, the P1 elicited by overlays of faces and

cars was indistinguishable whether attention was selectively engaged by the former or the latter. If enhanced attention to faces was responsible for the P1 modulation in Experiments 1 and 2, P1 amplitudes should have been different when faces and cars were presented in the relevant color because attended cars were systematically presented with a superimposed face. Manipulation of attention to faces also failed to modulate the amplitude of the N170, which is consistent with the view that selective attention does not modulate the P1-N1 complex^{12–14}.

Overall, these results stand in contrast with an interpretation of the N170 as a face-selective component^{1–8}. In the great majority of previous work, it can be assumed that ISPV was not explicitly controlled, as no mention of this variable was made. This leads to the possibility that category effects previously reported in the N170 range may be due in part to uncontrolled ISPV differences between experimental conditions. Furthermore, the sensitivity of the N170 to ISPV is consistent with hypotheses that the N170 is involved in higher integration processes that are not exclusive to faces, such as identification^{6,20}. Note, however, that detailed face identification mechanisms seem to be specifically indexed by even later components such as the N250r (refs. 21–23).

These results are difficult to relate to the intracranial recording literature. Face-selective responses from the inferior temporal lobe have been reported 200 ms after stimulus onset in individuals with intracortical electrode implants^{24,25}, although other reports indicate that face-related activity occurs as early as 50 ms after stimulus presentation^{26,27}. Comparisons between ERPs and intracranial recordings can only be tentative, as cortical activity in pharmacoresistant epileptic individuals may be affected by cognitive impairment following repeated seizures, intake of anticonvulsant medication or functional reorganization subsequent to the presence of epileptic foci^{20,25,28,29}.

We show that the N170 is highly sensitive to the degree of overlap between stimuli; that is, it is increased in amplitude when ISPV is low. This finding is compatible with the idea that the N170 reflects a viewpoint-dependent template matching process, such as that hypothesized to be implemented in the ventral extrastriate cortex³⁰. The modulation of the N170 by ISPV might thus result from a quantitative process reflecting the consistency (or synchronization) of neural responses across trials in the visual association cortex. When size, eccentricity and viewpoint are the same in different trials irrespective of the category of the object, the neural response elicited by highly similar perceptual events is highly consistent, and the resulting average ERP peak is increased in amplitude. Conversely, when ISPV is high across trials, dissimilar perceptual events elicit a less consistent neural response, and the average peak is reduced³¹. Based on the results of Experiment 2, this appears to be true even when only object size, eccentricity and proportions vary between trials.

Because the P1 showed the pattern of response that would have been expected from the N170 had it been selective for faces, and because the N170 scalp topographies were indistinguishable for faces whether ISPV was high or low, the P1 becomes *de facto* a better category sensitive ERP marker^{32,33}. These findings are consistent with the results of a previous EEG study that compared visual categorization of words and faces³⁴, or perception and nonperception of hidden faces¹¹. Similarly, results from MEG studies contrasting faces and degraded faces³⁵ or face categorization and identification²⁰ also indicate that face categorization takes place several tens of milliseconds earlier than was previously proposed based on ERP investigations. It remains to be determined, however, whether the category sensitivity in the P1 range is driven by low-level perceptual features of faces as compared with other objects. Such validation awaits systematic investigations using a wide range of object categories extending beyond the three categories used in the present

study. Furthermore, demonstrating genuine P1 category selectivity will require establishing a link between its cortical source(s) and the neural substrates traditionally associated with face processing.

The impact of ISPV in the results reported here has implications beyond the study of category specificity in visual object recognition. Our results suggest that ISPV needs to be controlled in any event-related design that does not use identical series of test items in every experimental condition (that is, that does not use stimulus repetition). This conclusion applies not only to ERPs and event-related magnetic fields, but also to event-related design in neuroimaging, as neural adaptation³⁶ is more likely to occur for a set of stimuli with low than high ISPV, thus inducing spurious hemodynamic response modulations in the opposite direction to those seen in ERPs.

METHODS

Experiment 1. Twenty-eight participants (mean age, 19.8 ± 2.1 years, 15 females, 3 left-handed) with normal or corrected-to-normal vision gave written consent to participate in the experiment that was approved by the ethics committee of the University of Wales, Bangor. One hundred pictures were collected from image databases for each of the following groups: (i) full front faces, (ii) faces varying in size, orientation, position and individual's age, (iii) full front cars and (iv) cars varying in size, orientation, position, make and manufacture period. All pictures were converted to black and white, and faces and cars were detoured and transposed on a medium gray (50% black) background. In the case of groups (i) and (iii), pictures were transformed to fit a predefined template to minimize ISPV (Fig. 2). In the case of groups (i) and (iv), half of the pictures were larger and half were smaller than the pictures in (i) and (iii) so as to balance average stimulus size. Stimuli were presented in pseudo-randomized order in four blocks of 100 trials such that each block featured 25 pictures from each of the four experimental conditions. It was therefore impossible for participants to predict what condition would be presented from one trial to the next. Five pictures in each block were randomly selected and presented twice (repetition trials). Participants were asked to press the space bar of a keyboard when they saw the exact same image twice in a row (one-back task).

Experiment 2. Twenty-seven participants (mean age, 20.1 ± 3.4 years, 19 females, 2 left-handed) viewed a randomized sequence of pictures pertaining to four conditions: (i) face profiles matched to a predefined template (low ISPV), (ii) the same faces reduced or magnified, moderately stretched or compressed along one axis, and randomly displaced off-center (high ISPV), (iii) side views of butterflies matched to a predefined template (low ISPV) and (iv) the same butterfly pictures, modified as in (ii). The face profiles were taken from the computer vision laboratory face database³⁷. All pictures were in black and white, detoured and transposed on a gray background. There were 80 different pictures in each condition. As in Experiment 1, it was not possible to predict the nature of the stimulus from one trial to the next and participants were asked to perform the same one-back task. Eight pictures in each block were randomly selected and presented twice.

Experiment 3. The same participants as in Experiment 2 viewed randomized sequences of pictures displaying overlays of full front faces and full front cars in two different colors (blue and green). Twenty of them (mean age = 19.3 ± 1.0 , 14 females, all right-handed) were included in the ERP analysis based on their performance (see Results). Source pictures were the same as those used in conditions (i) and (ii) of Experiment 1 and therefore had comparably low ISPV. The same faces and cars were presented twice in blue and twice in green across the experiment, albeit paired with a different stimulus in the two instances, and never in the same experimental block. Participants were asked to detect blue image repetitions in two blocks of trials and green image repetitions in two other blocks. They were instructed to ignore the other color. Stimulus distribution between blocks was programmed such that specific faces and cars presented in each of the attended color conditions always had the same color (Fig. 3). In other words, the stimulus pools presented in the attend blue and attend green condition differed on the basis of color. By contrast, the stimulus pools presented in the attend face and attend car conditions (as a

result of attending one given color) were perceptually identical, because attended objects were presented once in blue and once in green across the experiment (Fig. 3). Stimulus succession was pseudo-randomized such that the color, category or identity of the object was unpredictable from one trial to the next. The order of participation in Experiments 2 and 3 was counter-balanced between participants.

Event-related potentials. Scalp activity was digitized at a 1-kHz sampling rate from 64 Ag/AgCl electrodes distributed throughout the scalp according to the 10–20 convention using Cz as a reference. Impedances were kept below 7 kOhms. The electroencephalogram was filtered on-line between 0.01 and 200 Hz and off-line low pass at 35 Hz using a zero phase-shift digital filter. Eye blink artifacts were mathematically corrected, and signals exceeding ± 75 μ V in any given epoch were automatically discarded. Continuous recordings were cut into epochs ranging from –100 ms to 500 ms after stimulus onset and averaged for each individual in each of the four experimental conditions. Repetition trials necessary for the one-back task were systematically excluded from averaging. Grand averages were calculated after re-referencing individual ERPs to the common average reference. Peak amplitudes were analyzed at the ten most posterior parietooccipital electrodes; that is, PO3, PO4, PO7, PO8, PO9, PO10, POz, O1, O2 and Oz were analyzed by a $2 \times 2 \times 10$ repeated measures ANOVA. In Experiment 1 and 2, the factors were category (face/car or face/butterfly), ISPV (low, high) and electrode (10 levels). In Experiment 3, the factors were attended color (blue/green), attended category (face/car) and electrode (10 levels). A Greenhouse-Geisser correction was used where applicable.

Segmentation and source analysis. The series of maps constituting an ERP does not fluctuate randomly, but is characterized by periods of relative stability lasting for tens to hundreds of milliseconds^{38–40}. These periods of stability have been termed functional microstates and are thought to correspond to steps in information processing during which a brain region or network remains active^{11,38,39,41}. To identify these microstates, we used a spatial k-means cluster analysis that identifies the dominant topographies, or segment maps, that account for the greatest amount of variance in the ERP map series⁴². The optimal number of segment maps and their times of occurrence are selected on the basis of a cross validation criterion in which the smallest number of segment maps explaining the greatest amount of variance is retained. Segment map selection is therefore purely data-driven. Scalp topographies may be identical yet vary with respect to their strength. Such intensity differences can be measured by computing the global field power. The latter is a measure of the spatial s.d. of the scalp potential and provides a unique value at every time point that increases with a greater spread of negative and positive potentials⁴³.

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AUTHOR CONTRIBUTIONS

G.T. conceived Experiments 1 and 3, analyzed ERP data of Experiment 1, supervised overall data analysis and wrote the manuscript. C.D.M. conceived Experiment 2 and analyzed ERP data of Experiment 2 and 3. P.D. performed pixel-wise correlation analyses, provided expertise on neuroanatomical interpretations and wrote parts of the manuscript. A.J.P. performed the segmentation analyses and wrote parts of the manuscript.

COMPETING INTERESTS STATEMENT

The authors declare no competing financial interests.

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