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Research Report

Invariance to rotation in depth measured by masked repetition priming is dependent on prime duration

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ABSTRACT

The current experiment examined invariance to pictures of objects rotated in depth using event-related potentials (ERPs) and masked repetition priming. Specifically we rotated objects 30°, 60° or 150° from their canonical view and, across two experiments, varied the prime duration (50 or 90 ms). We examined three ERP components, the P/N190, N300 and N400. In Experiment 1, only the 30° rotation condition produced repetition priming effects on the N/P190, N300 and N400. The other rotation conditions only showed repetition priming effects on the early perceptual component, the N/P190. Experiment 2 extended the prime duration to 90 ms to determine whether additional exposure to the prime may produce invariance on the N300 and N400 for the 60° and 150° rotation conditions. Repetition priming effects were found for all rotation conditions across the N/P190, N300 and N400 components. We interpret these results to suggest that whether or not view invariant priming effects are found depends partly on the extent to which representation of an object has been activated.

1. Introduction

An often debated topic in the field of object recognition is whether recognition is viewpoint dependent or not. Viewpoint independent recognition refers to the ability to recognize objects from various viewpoints equally well. Whereas, viewpoint dependent recognition refers to difficulty recognizing objects from less familiar viewpoints or ones that are different from the reference/canonical viewpoint of an object. The ability to rapidly discriminate objects from one another as well as recognize objects as the same under various viewing conditions relies upon being able to establish a representation that is sufficient to perform this difficult task.

One paradigm typically used to determine viewpoint dependent or independent recognition is priming. In priming, an object is presented (the prime) and followed, either immediately or with some delay, by a repeated object or unrelated object (the target). When objects are repeated accuracy is higher and reaction times faster to the target object compared to unrelated targets. Typically, viewpoint dependent recognition is characterized behaviorally by decreased accuracy or increased reaction time when an object is primed by the same object in a different viewpoint than the target object to be recognized in comparison to when the same viewpoints are presented as prime and target. Viewpoint independent recognition occurs in priming when there is no difference in reaction time and accuracy when the target object is a different

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viewpoint than the prime object. In addition, viewpoint dependent recognition may be associated with particular patterns of brain activity, where rotation from the original viewpoint to another viewpoint leads to increase brain activity (recovery from adaptation) or in the case of viewpoint independent recognition, a decrease in brain activity (repetition suppression or adaption).

The current experiments aimed to use event-related potentials (ERPs) to uncover how perceptual, form specific and semantic object representations are sensitive to orientation information by using a technique typically employed in behavioral object recognition studies: priming. Perceptual representations of objects are rapidly activated and may be less sensitive to viewpoint, whereas, more detailed, high level form specific and semantic object representation activations may be disrupted more by changes in viewpoint, especially when the exposure to the stimulus is relatively brief. Importantly though, we are examining the timecourse of the processes involved in activating an object representation rather than the outcome of these processes such as recognition, typically examined in behavioral studies. While the recognition of rotated objects has been extensively studied, there is a limited understanding of the mechanism that leads to this viewpoint dependent or viewpoint independent recognition. The current experiments aimed to better understand the nature of the *representation* that underlies object recognition processes by obtaining timecourse information about the stimulus attributes that are important during object processing.

Several theories of object recognition, based primarily on behavioral outcomes such as reaction time or accuracy, propose mechanisms that support either view-invariant or view-dependent object recognition on the basis of how objects are represented. According to theories of view-invariant recognition, recognition is accomplished through mechanisms of recoverable parts (Biederman, 1987) or generalization of cylinders (Marr, 1982) whereas recognition in view-dependent theories is accomplished through a representation composed of multiple views (e.g., Bülthoff and Edelman, 1992; Tarr, 1995). View-invariant recognition is established through interpolation across these stored views. Previous behavioral studies have found evidence for both perspectives, although the majority of findings seem to suggest a more view-dependent recognition mechanism. However, as pointed out by several authors (e.g., see Harris et al., 2008; Hummel, 2000) the ability to recognize an object in a view-point invariant fashion and how the object is represented are not necessarily the same the thing. Neuropsychological studies provide evidence that often times object structural or shape information is activated prior to orientation information such as those patients who can recognize objects but not determine their orientation (Harris et al., 2001; Turnbull et al., 1996), suggesting the underlying representation can be activated independent of orientation.

With the advent of fMRI, many studies have addressed wherein the brain objects are represented in a view invariant/dependent way. One technique used to examine this question is the fMRI adaptation paradigm (fMRI-A) where the amount of recovery from adaptation is taken to reflect the degree of overlap between representations of the first and second stimulus presented (e.g., Grill-Spector et al., 1999; Vuilleumier et al., 2002). More overlap between the two stimuli is indicated by more adaptation (reduction in the neural signal as measured by the BOLD response). Typically these studies have found lack of adaptation in fusiform and lateral occipital cortex when objects are rotated in depth (e.g., Grill-Spector et al., 1999; Vuilleumier et al., 2002) which has been interpreted as suggesting that these brain areas do not represent objects in a way that is independent of viewpoint. However, Vuilleumier et al. (2002) did find that the left anterior and posterior fusiform gyrus did exhibit adaptation when an object was rotated, indicating that the left fusiform gyrus presumably represents objects in a more view independent fashion. In addition James et al. (2002) defined a region of interest within the LOC that was highly correlated to activation to intact objects compared to scrambled objects on the temporal–occipital boundary of the fusiform gyrus, which they termed the ventral temporal–occipital area (vTO). Within the vTO they found the same amount of reduced activity to repeated different views of objects as repeated same views of objects. When the vTO was made larger to include the whole LOC, a similar pattern to the viewpoint dependent results found by Grill-Spector et al. (1999) were found suggesting that the LOC is heterogeneous in its generalization of object viewpoint.

However, because fMRI lacks precise temporal resolution, it is difficult to disentangle the role of recurrent and feedforward processing in the obtained adaptation effects especially where the time between the first and second presentation of the stimulus has typically included variable lags (Andresen et al., 2009). Applying the technique of ERPs to this question is particularly relevant given these limitations of fMRI and the often contradictory findings from previous behavioral studies where evidence against invariance in recognition has been reported (e.g., Bülthoff and Edelman, 1992; Hayward and Tarr, 1997; Tarr, 1995) and has been used to infer the representation leading to recognition must be view-dependent. ERPs can help further explain these findings by providing a continuous measure of the processes underlying recognition. In addition, ERPs have previously been shown to be sensitive to view and size manipulations with objects (Eddy and Holcomb, 2009) as well as unusual viewpoints (Schendan and Kutas, 2003), proving useful to further understand object representations. Therefore, we proposed to use a particular type of priming, masked repetition priming, with ERPs to examine the processing of stimuli that overlap in object identity, but have different orientations.

The repetition priming technique, which is very similar to the fMRI adaptation paradigm, has been used extensively to probe the timing of fast, automatic recognition. One variant of this technique, masked repetition priming, has proven to be quite useful for helping disentangle the component processes involved in visual word recognition. And recently, this formerly behavioral technique has been adapted for use with ERPs. Masked repetition effects in ERPs rely upon the same principles as adaptation in fMRI: an increase in ERP amplitude to a target stimulus that varies on some physical dimension from the prime stimulus compared to an identity repetition of this stimulus has been argued to reflect the relative lack of invariance in the identity condition. Throughout the rest of this paper, we will refer to the difference in ERP amplitude produced by priming, where repeated trials show less amplitude than unrepeated, as “repetition effects” which is analogous to “adaptation effect” in fMRI.

Henson (2003) in his review of priming techniques, points out that one of the benefits of masked priming over supraliminal paradigms that rely on implicit priming is that explicit influences can contaminate target processing in supraliminal tasks. In masked priming, the participant has limited access to the prime and therefore, explicit processes are greatly attenuated as demonstrated by reduced frontal activation in masked priming with words in fMRI (see Dehaene et al., 2001). Therefore with masking, the observed effects are generally assumed to be perceptual (see Misra and Holcomb, 2003). In fact, it seems likely that masked priming largely involves fast feed-forward processing as single unit recordings in monkeys have shown that recurrent processing of a stimulus is blocked by masking (Lamme et al., 2002). Specifically, Lamme and colleagues found that recurrent processing in V1 is blocked when a target presented for 14–110 ms is immediately backward masked by a 300 ms pattern mask. Isolating processes involved in perceptual processing of stimuli is ideal when the aim is to study perceptual variations in stimuli (such as rotations in depth) where a strategy may be implemented in processing the stimuli under supraliminal presentations.

Using masked priming and ERPs to examine at precisely which points in time stimulus rotation is processed should be possible because previous ERP masked priming studies have broken down the different stages in word recognition processes (see Grainger and Holcomb, 2009). In one previous study we used masked repetition picture priming combined with the recording of ERPs to probe changes in size and mirror reflection (see Eddy and Holcomb, 2009). In that study we found invariance to size, as indicated by a reduction in the ERP repetition effects (reduced ERP amplitude for repeated compared to unrepeated trials), for both early perceptual (N/P190) and later semantic (N300/N400) ERP components. However, only the perceptual component showed invariance to mirror reflection. The pattern of N/P190 repetition effects found in this study suggest that mirror reflected objects can be represented in a perceptually invariant fashion (on the basis of low level visual features) with a brief (50 ms) exposure. However, left–right orientation mismatch of the object incurs a cost in higher levels of processing, indicated by reduced repetition effects on the N300 and N400 components. Overall, when objects are mirror reflected, the low level perceptual representation is not sensitive to the mirror reflection, however, more elaborate, higher level representations are sensitive to the mirror reflection. Because these components showed less of a difference between repeated and unrepeated trials, suggests that more neural processing is required for mirror stimuli even when the prime and the target share the same identity. This interpretation was favored over one proposing that additional processing time was required because if this was the case, we would have expected a delay as opposed to an absence of repetition effects.

In addition to the extensive behavioral literature that would suggest increased processing demand with rotation in depth (e.g., Tarr, 1995; Tarr et al., 1997), ERP evidence for an increased demand in neural processing comes from research by Schendan and Kutas (2003). They showed that unusual views of objects lead to larger increases in ERP amplitude compared to more canonical views of objects, possibly indicating the operation of a mechanism to normalize one view of the object or match it with a stored representation. They also observed an N350 effect, presumably similar to the N300 or N400 reported by others that had a more negative-going amplitude for unusual views of objects than canonical views. They attributed the sensitivity of a late posterior negativity to viewpoint, which was larger for unusual views than for canonical views of studied objects, as being consistent with the idea of a compensation process such as mental rotation being necessary for recognition (for an argument against mental rotation in recognition of rotated objects see Gauthier et al., 2002). Given the supraliminal nature of their stimuli (during the study phase objects were presented for 5 s or until a response was made) and the study-test design (there was a lag of 10 min between study and test), the results from Schendan and Kutas' (2003) study cannot be exclusively attributed to perceptual processes involved activating the object representation.

1.1. *The current study*

The aim of the current experiments was to examine how changes in orientation (rotation in depth) and duration of prime presentation affect ERP components specific to object recognition processes. While behavioral and fMRI studies have elucidated to some extent the mechanisms underlying invariant or view-point dependent recognition, more information about the time-course of these processes is necessary. ERPs combined with masked priming appear to be the ideal methodology for isolating the contribution of fast feed-forward mechanisms to these processes.

In this experiment we briefly presented (50 ms) pattern masked pictures of objects that were rotated 30°, 60° or 150° from the canonical view. These “prime” objects were then followed by a longer duration “target” object presented from the canonical viewpoint. Targets were either the same object as the prime or an unrelated object (see Fig. 1). Participants performed a semantic categorization task where they were asked to press a button to non-critical, occasional food pictures. The critical conditions for this experiment contained non-probe pictures. ERPs were recorded from 29 scalp electrodes with the recording referenced to the left mastoid (see Fig. 2 for electrode layout).

1.2. *Experiment 1*

For the first experiment where we manipulated object rotation in depth, we predicted the following pattern of repetition effects:

1. *N/P190 effect*: Because this effect presumably reflects perceptual overlap (features such as shape or local features) between the prime and target, this effect should be observed regardless of the amount of rotation. This is consistent with Eddy and Holcomb's (2009) findings where mirror reflected (equivalent to 180° rotation) produced significant N/P190 repetition effects, even though this effect was slightly smaller than the N/P190 for identity priming (likely

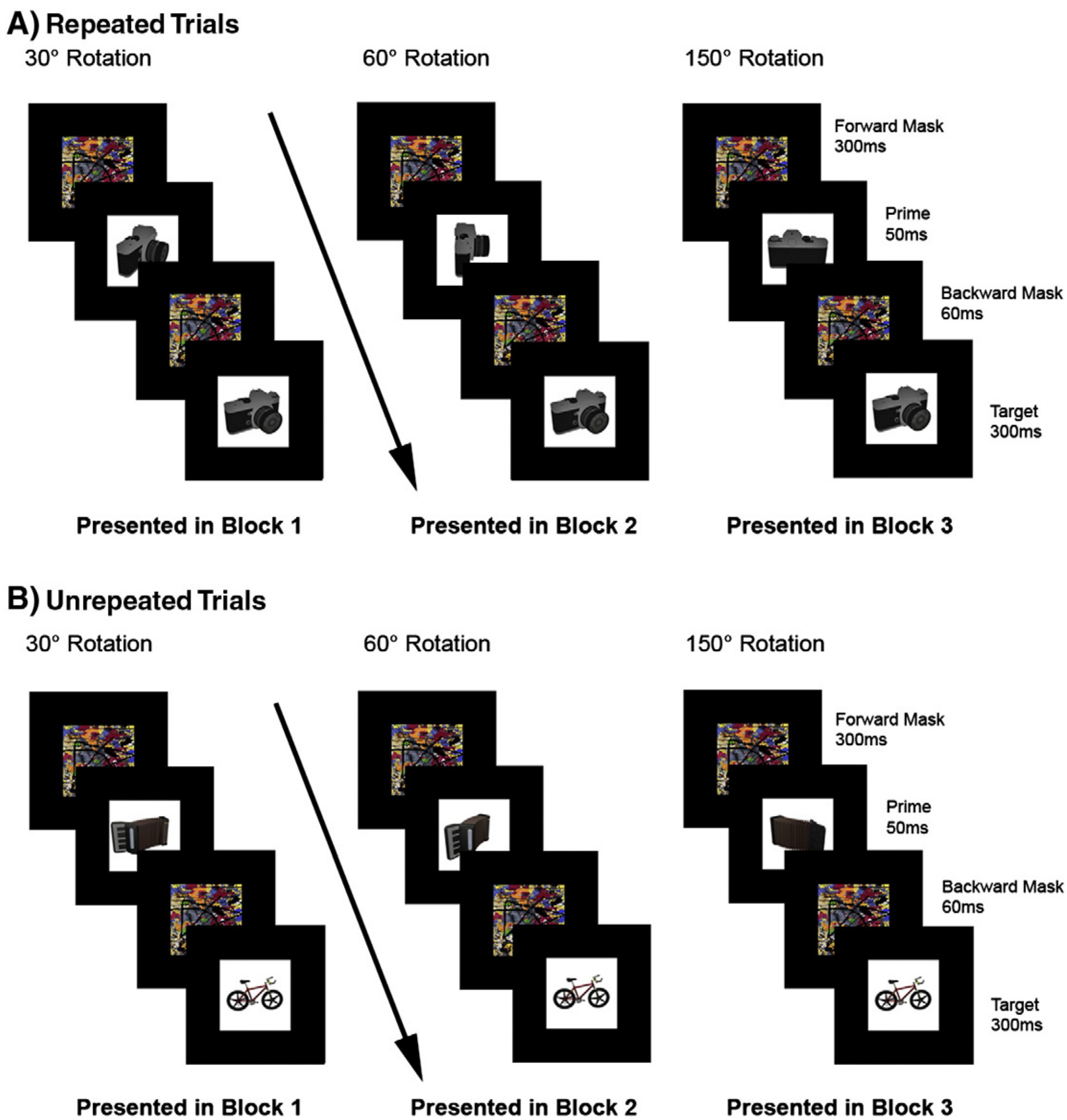

Fig. 1 – Example of typical trials.

because there is not a one-to-one match of perceptual features in the mirror reflected condition, whereas the identity priming condition is perceptually identical). Even when the target object is rotated, in comparison to the unrepeated condition, the repetition condition will still have more perceptual overlap. It has been speculated that this effect is generated by posterior fusiform cortices, but in fMRI adaptation paradigms this region does not show adaptation. However, recall that it is difficult to disentangle feed-forward and feed-back contributions as well as contributions of subareas of neurons within this region; therefore, we still predict repetition effects across all degrees of rotation on this ERP component due to overlapping perceptual features.

2. *N300 effect*: More consistent with previous fMRI findings and with the suggestion that the N350 described by Schendan and Kutas (2003) may have generators in the fusiform cortex and LOC, we predict that this component, presumably sensitive to object level form representations, will only be observed when the prime object is rotated a small amount. Because higher level properties of the object representation, (those having to do with overall object form) are presumably important, this overlap in representation is disrupted when the object is rotated in depth. Therefore we predict N300 repetition effects for only the 30° condition and none for the 60° and 150° conditions. This prediction would also be consistent with the idea of viewpoint dependent object recognition where sufficient information is needed to match up the presented view with the target view of the object.
3. *N400 effect*: The N400 reflects semantic integration processes across a wide variety of stimulus types and therefore, a higher level abstract process. If sufficient processing of the object form leads to activation of this higher level representation, we predict an N400 effect should be observed. Since we predict that only the 30° condition will produce N300 repetition effects, we also then would predict that only this condition will show N400 repetition effects, since the other degrees of rotation do not lead to sufficient form overlap to activate a higher level representation of

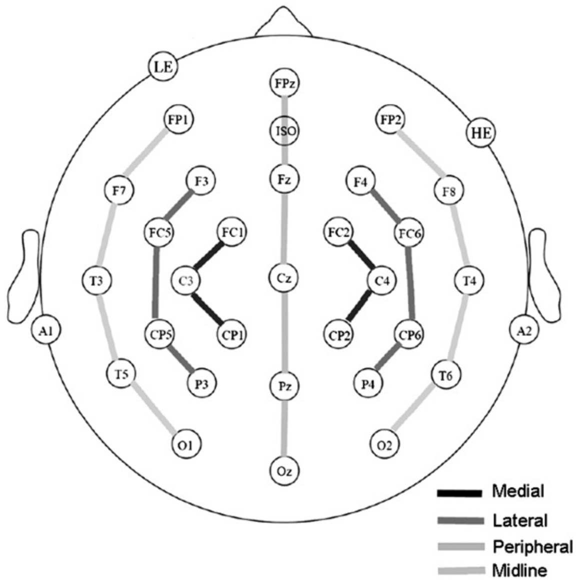

Fig. 2 – Electrode montage for 29 channel EEG recording.

the object. One could speculate that the N400 may be produced by recurrent processing. If this is the case, we would expect N400 repetition effects across all degrees of rotation, regardless of the form overlap. We do not expect this pattern, however, since in a previous study, mirror reflection of the prime object disrupted N400 repetition effects and because the prime is being presented for a brief duration (50 ms) and backward masked, reducing or eliminating recurrent processes.

2. Results

2.1. *Experiment 1 results*

This experiment examined the effect of rotating the prime object in depth on processing of conventional views of target objects. We examined how the N/P190, N300 and N400 repetition priming effects were modulated by rotating objects 30°, 60° and 150° in depth from the conventional view of that object. Behavioral accuracy was indexed by d' scores calculated for detecting food probe items in the target position. A d' value of 4.39 for target food items demonstrates that participants accurately performed the semantic categorization task.

A visual inspection of the ERPs (see Figs. 3A–C) shows intact repetition effects at all time windows when a conventional target is primed by a 30° rotation of this object. However, rotations of 60° and 150° seem to disrupt target processing in the N300 and N400 time windows, while the N/P190 effect remains intact. For each component, we examined the effect of Degree of Rotation, Repetition, Electrode site, and Hemisphere (with the exception of the midline column) as well comparisons for 30°, 60°, and 150° conditions separately, where interactions from the initial ANOVA warranted further comparisons. The 29 scalp electrodes were divided into four columns with the factors of electrode site and hemisphere (except the midline): midline (Fz, Cz, Pz, Oz), medial (FC1–FC2, C3–C4, CP1–CP2), lateral (F3–F4, FC5–FC6, CP5–CP6, P3–P4) and peripheral (FP1–FP2, F7–F8, T3–T4, T5–T6, O1–O2) for the analysis and the statistics are reported separately for the columns. The medial, lateral and peripheral electrodes are listed in pairs by hemisphere (left–right) whereas the midline column does not have the factor of hemisphere, only electrode site, which is listed anterior to posterior.

2.1.1. *N/P190 epoch (100–250 ms)*

The initial ANOVA including the factors of Degree of Rotation, Repetition, Electrode, and Hemisphere (except midline) showed main effects of Repetition (midline: $F(1,23)=14.365$, $p=0.001$, $\eta_p^2=0.384$; medial: $F(1,23)=22.101$, $p=0.000098$, $\eta_p^2=0.490$; lateral: $F(1,23)=16.537$, $p=0.0005$, $\eta_p^2=0.418$) as well as a Repetition × Electrode Site interactions (midline: $F(4,92)=25.901$, $p=0.0000004$, $\eta_p^2=0.530$; medial: $F(2,46)=11.771$, $p=0.001$, $\eta_p^2=0.339$; lateral: $F(3,69)=21.141$, $p=0.00002$, $\eta_p^2=0.479$; peripheral: $F(4,92)=32.710$, $p=0.00000015$, $\eta_p^2=0.587$) across all rotation conditions. These effects did not interact with Degree of Rotation. In all conditions, the Repetition × Electrode Site interaction was reflected in the N190 (anterior)/P190 (posterior) change in the polarity of this effect from anterior to posterior electrodes. As typically seen, the anterior effect shows greater negativity for unrepeated compared to repeated trials, whereas the posterior effect has a greater positivity for unrepeated compared to repeated trials. This difference however, did not interact with Degree of Rotation; therefore follow-up comparisons were not performed.

2.1.2. *N300 epoch (250–350 ms)*

An ANOVA including Degree of Rotation, Repetition, Hemisphere (except midline), and Electrode site revealed an interaction between Degree of Rotation × Repetition × Hemisphere in the medial column ($F(2,46)=4.018$, $p=0.028$, $\eta_p^2=0.149$). This interaction was driven by the 30° rotation condition having a greater negativity for unrepeated compared to repeated trials that is larger in the right hemisphere, whereas the 60° and the 150° conditions did not show this effect (see Figs. 3A–C; 4B). In this initial ANOVA there was also a significant interaction between Degree of Rotation, Repetition and Electrode Site (lateral: $F(3,69)=4.335$, $p=0.026$, $\eta_p^2=0.159$, peripheral: $F(4,92)=4.28$, $p=0.018$, $\eta_p^2=0.157$). Follow-up comparisons were performed for each of the degree of rotation conditions separately with the factors of Repetition, Electrode Site, and Hemisphere to further examine these effects. Only the 30° condition showed repetition effects. The effects for this condition had an anterior distribution (see voltage maps Fig. 4 for 30° condition) as indicated by Repetition × Electrode Site interactions (midline: $F(4,92)=3.962$, $p=0.018$, $\eta_p^2=0.147$; lateral: $F(3,69)=5.94$, $p=0.008$, $\eta_p^2=0.205$; peripheral: $F(4,92)=9.176$, $p<0.0001$, $\eta_p^2=0.285$). For the 60° condition there were no significant main effects or interactions with Repetition (all $Fs<1.3$, all $ps>0.27$). There was a trend towards a significant main effect of Repetition for the 150° condition (midline: $F(1,23)=3.144$, $p=0.089$, $\eta_p^2=0.120$) however, this effect was in the opposite direction of the typical N300 effect (see voltage maps in Fig. 4).

2.1.3. *N400 epoch (350–500 ms)*

In the initial ANOVA including the factors of Degree of Rotation, Repetition, Electrode Site and Hemisphere (except for the midline column) there was an interaction between Degree of Rotation × Repetition × Electrode Site interaction at the peripheral electrode column (F(8,184) = 3.049, p = 0.036, η_p^2 = 0.117). The same ANOVA also produced a significant main effect of Repetition (medial: F(1,23) = 4.294, p = 0.050, η_p^2 = 0.157; lateral: F(1,23) = 4.290, p = 0.050, η_p^2 = 0.157). To further examine the effect of rotation on repetition, follow-up analyses examining repetition effects for each condition were performed separately. Only the 30° condition showed significant repetition effects as indicated by main effects of Repetition (midline: F(1,23) = 3.715, p = 0.066, η_p^2 = 0.139 (trend); medial: F

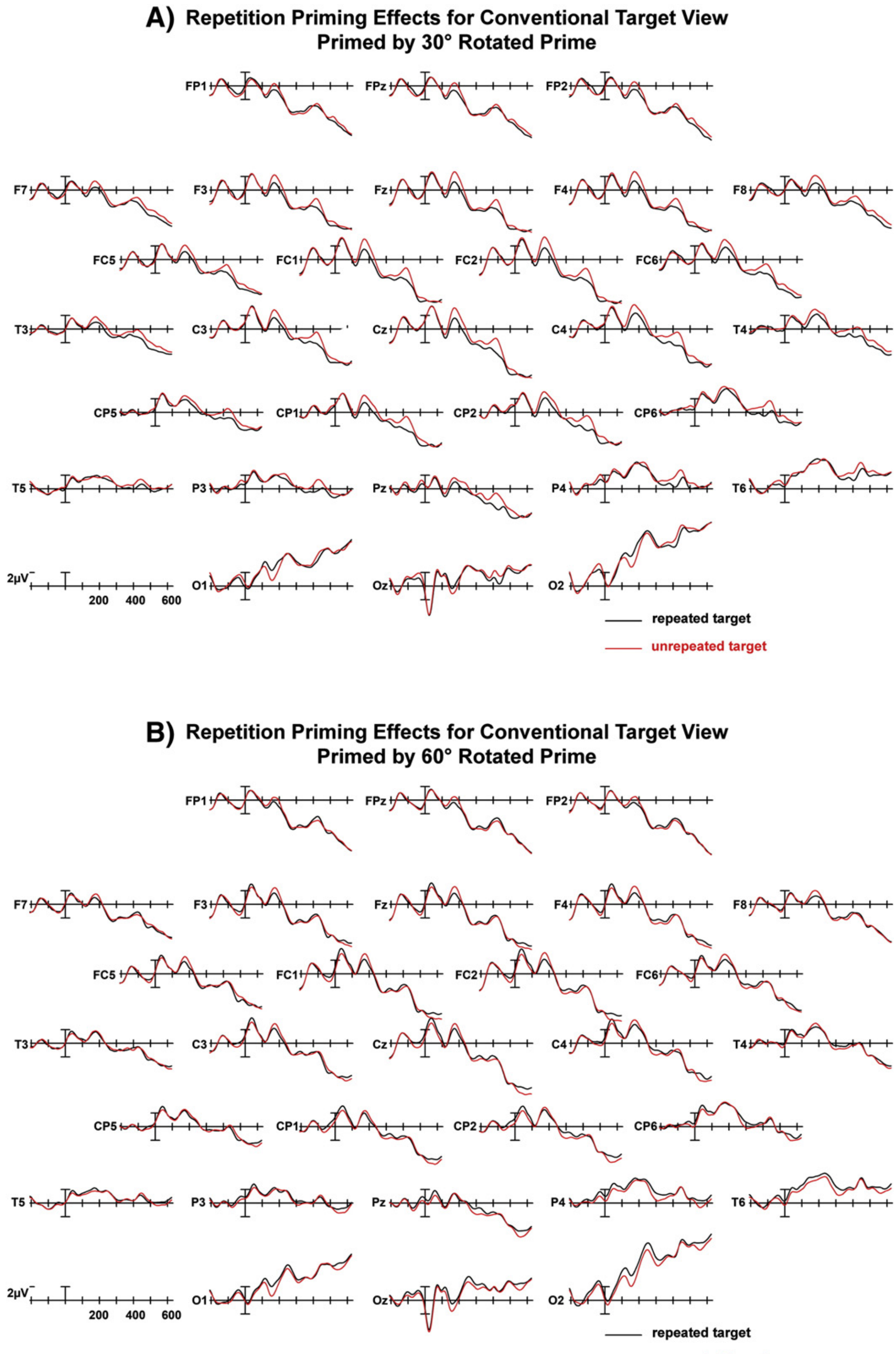

Fig. 3 – Experiment 1: grand average ERPs (N = 24). Red = unrepeated trials, Black = repeated trials. Note that negative is plotted up.

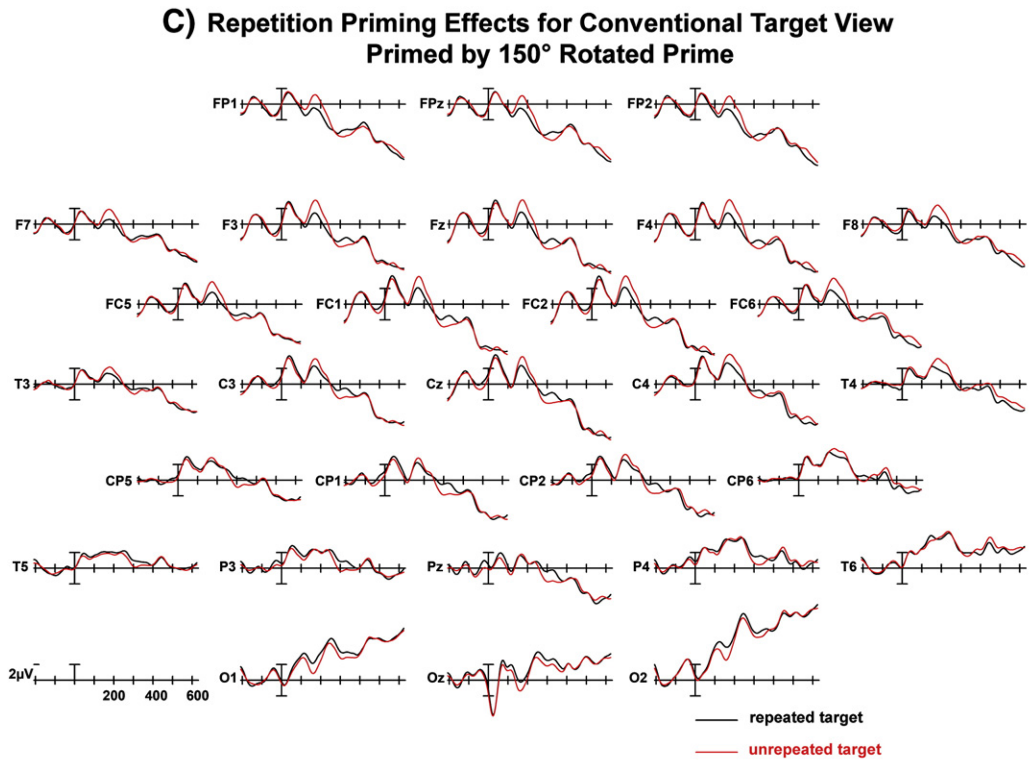

Fig. 3 (*continued*).

(1,23) = 4.989, p = 0.036, $\eta_p^2 = 0.178$; lateral: F(1,23) = 6.888, p = 0.015, $\eta_p^2 = 0.230$; peripheral: F(1,23)–6.425, p = 0.019, $\eta_p^2 = 0.218$). No significant effects were observed for the 60° or 150° conditions (all Fs < 2.3, all ps > 0.14).

2.2. *Discussion of Experiment 1*

We predicted that repetition effects would become increasingly sensitive with time to rotation with the N/P190 being least sensitive (and therefore showing the largest repetition effects) and the N300 and N400 being more sensitive to rotation. Specifically it was predicted that rotation in depth of the prime object, during the early stages of object processing (as indexed by the N/P190) would not disrupt repetition effects on the target object. And indeed there were no differences between the 30°, 60° and 150° conditions on the early N/P190 repetition effect. However, during later object processing stages, where whole object form and mapping from this form to semantics are important, only the 30° condition continued to produce repetition effects. These stages of processing were indexed by the N300 (form processing) and the N400 (semantic integration) processes. The idea that form overlap is necessary to activate higher level representations is consistent with a hierarchical processing of object attributes as well as theories suggesting that recognition is viewpoint dependent. Because these higher level processes are more likely contributing to the response in behavioral studies (object naming, object matching), the findings of reduced repetition effects on these components may be related to those behavioral studies finding viewpoint dependent recognition.

While effects were observed for early perceptual processing for all degrees of rotation, the higher level processes reflected by the N300 and N400 repetition effects appear to need an intermediary representation or overlap in higher level features beyond mere perceptual overlap, as N300 and N400 effects were not significant in the 150° rotation condition or the 60° rotation condition. Only the 30° rotation condition showed significant priming effects for the N300 and N400. The finding of viewpoint invariance with a small rotation in depth is consistent with predictions that generalization across viewpoints occurs with small rotations (less than 40°, see Logothetis et al., 1994; Poggio and Edelman, 1990). A higher level representation for the 30° rotation condition may be activated by the overlap of shape and part features of the prime and target objects, since the 30° rotation produces very little change in the perceptual properties between the prime and conventional view in the target position.

It does seem contradictory that invariance can be found at an early stage of processing, but not at a later stage(s). However, because the representation reflected by the N/P190 likely reflects low level overlap (one-to-one correspondence of shape, or feature matching) that are less sensitive or fine-tuned representations and the N300 and N400 require more elaborate detail to activate the higher level representation reflected by them (e.g., more fine-tuned, sensitive representations) it is conceivable that this pattern of effects could be observed. It is possible that the viewpoint independent priming in the N/P190 reflects a similar process as that in vTO in the James et al. (2002) study, where viewpoint independent effects were found in a more inferior part of the LOC (termed the vTO) and viewpoint dependent effects were found when the region was extended to include the whole LOC. The activation in the LOC could represent the mapping of the viewpoint independent perceptual representation to a higher level form specific representation in the LOC.

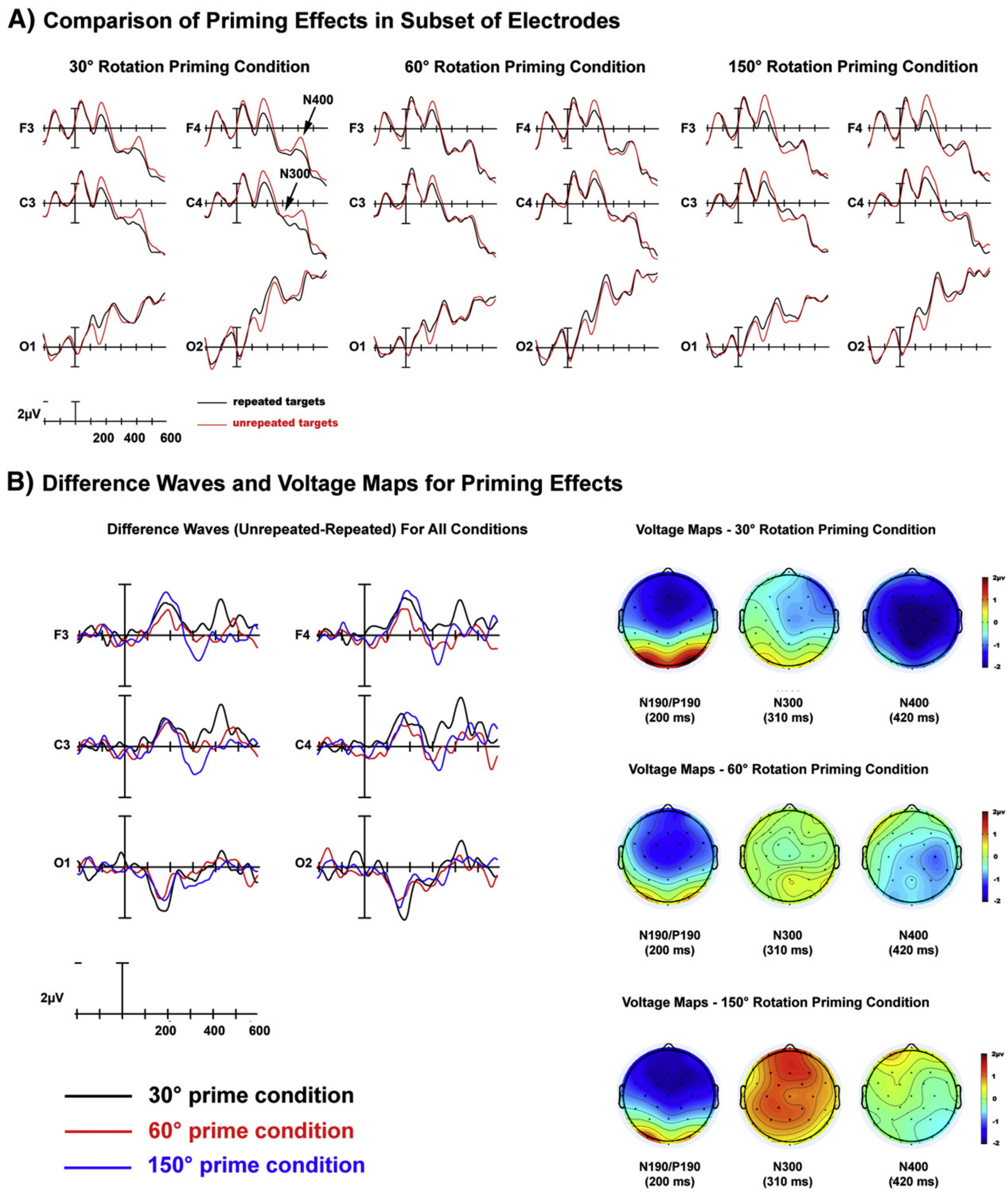

Fig. 4 – Experiment 1: (A) subset of electrodes and (B) voltage maps. Voltage maps show unrepeated – repeated voltage differences. Note that negative is plotted up.

The lack of N300 and N400 repetition effects with increased rotation suggests that while the hypothesis put forward by Bar (2003) for top–down facilitation in recognition may underlie some instances of object recognition, it is unlikely in our particular paradigm that a top–down facilitation accounts for the repetition effects observed. There are two reasons for this: the first being that the initial presentation of the prime may very well lead to some top–down activation; however it is unlikely that this activation will persist and lead to adaptation of the same neurons during the second presentation of the stimulus. This is because of the brief prime exposure and immediate presentation of the backward mask, which has been shown to cut-off recurrent processing (Lamme et al., 2002). Secondly, using the same masked repetition priming procedure in fMRI (although not with rotations in depth) Eddy et al. (2007) found no evidence for repetition suppression effects outside the fusiform gyrus. These findings do not eliminate the possibility that top–down feedback plays a role in object recognition, but do suggest that the repetition effects we observed with ERPs using masked priming are not likely produced by top–down facilitation.

Another variable possibly affecting our findings is the prime exposure. It is possible with a longer prime exposure that more recurrent processing would occur, providing

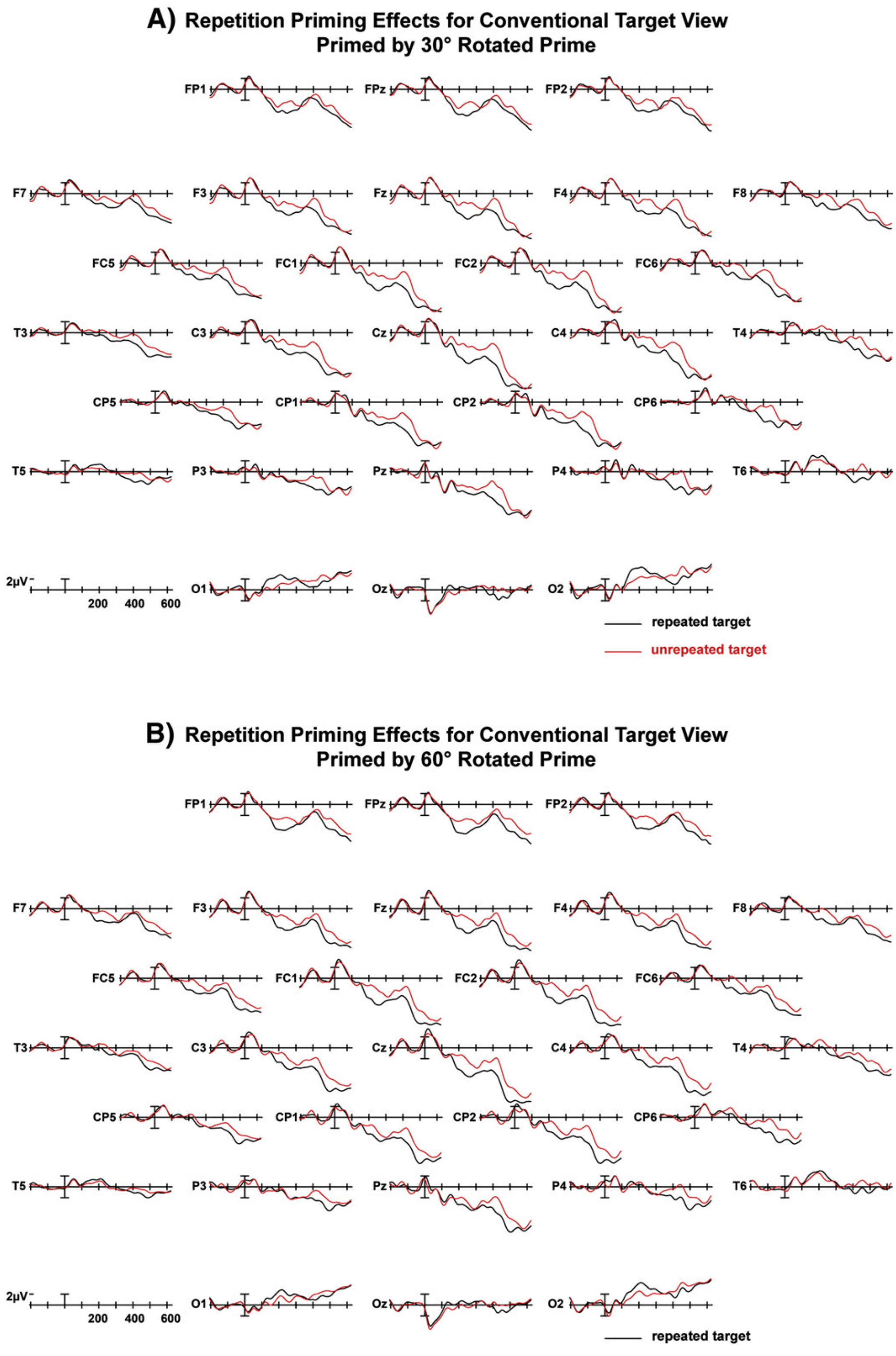

Fig. 5 – Experiment 2: grand average ERPs (N = 24). Red = unrepeated trials, Black = repeated trials. Note that negative is plotted up.

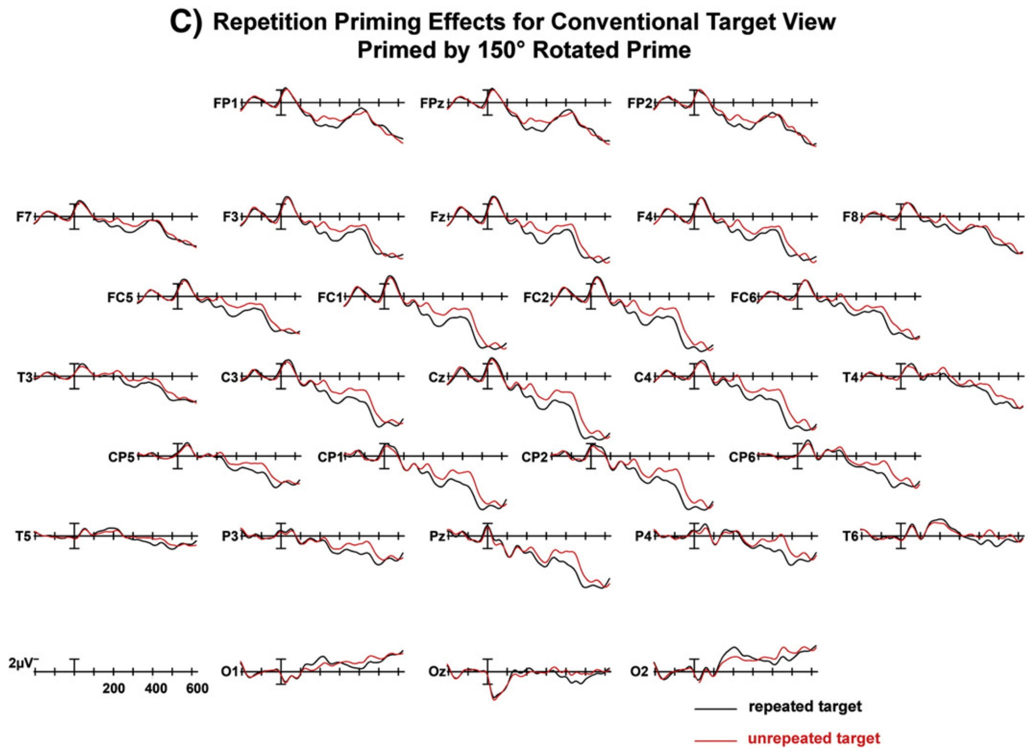

Fig. 5 (*continued*).

sufficient activation along the ventral visual stream to produce higher level priming effects. We have previously found more robust priming effects when extending the prime duration to 70 and 90 ms (Eddy and Holcomb, 2010).

2.3. *Experiment 2*

One reason that repetition effects (N300 and N400) were not found in Experiment 1 is that the very brief presentation of the masked rotated primes did not allow enough time for a robust representation of the prime form and thus might have attenuated some of the ERP effects of rotation because of the reliance on mainly perceptual features of the stimuli. The aim of the second experiment was to examine if the increase in prime exposure allows a higher level, more abstract representation of the rotated prime object to be activated that produces invariance in masked repetition effects in ERPs. We increased the prime duration from 50 ms to 90 ms, while keeping the SOA constant (at 110 ms) by changing the backward mask duration from 60 ms to 20 ms and presented the same stimuli as in Experiment 1 to a different group of participants, while once again recording ERPs. This allows us to examine if the increase in prime exposure allows a higher level, more abstract representation of the rotated prime object to be activated that produces invariance. Previous studies using ERPs and manipulating the prime duration have shown that increasing the prime duration leads to enhanced N400 effects in masked repetition priming (see Eddy and Holcomb, 2010; Holcomb and Grainger, 2006). We predicted that increasing the prime duration would allow for a more robust representation to be activated, leading to repetition effects (N300 and N400 effects) for all degrees of rotation.

2.3.1. *Results of Experiment 2*

Behavioral accuracy, as indexed by d' scores for detecting food probe items in the target position was similar to those in Experiment 1. A d' value of 4.45 for target food items demonstrates that participants accurately performed the semantic categorization task.

Visual inspection of the grand average ERPs (see Figs. 5A–C) reveals a different pattern of priming effects than those observed in Experiment 1. Across all three rotation conditions, clear N/P190, N300 and N400 effects are evident. Statistical comparisons performed confirmed these visual observations.

2.3.1.1. N/P190 epoch (100–250 ms). The overall ANOVA including all three degrees of rotation and repetition revealed main effects of repetition (midline: $F(1,23)=15.507$, $p=0.001$, $\eta_p^2=0.403$; medial: $F(1,23)=22.514$, $p=0.00009$, $\eta_p^2=0.495$; lateral: $F(1,23)=10.492$, $p=0.004$, $\eta_p^2=0.313$) and interactions of repetition and electrode site (midline: $F(4,92)=24.715$, $p=0.000001$, $\eta_p^2=0.518$; medial: $F(2,46)=10.512$, $p=0.002$, $\eta_p^2=0.314$; lateral: $F(3,69)=21.605$, $p=0.000002$, $\eta_p^2=0.484$; peripheral: $F(4.92)=40.623$, $p=0.00000005$, $\eta_p^2=0.638$), but no interaction of repetition by degree of rotation, confirming that this effect did not differ for degree of rotation (all $Fs<1$, $ps>0.1$, $\eta_p^2<0.1$). The interaction of repetition and electrode site is reflected by the change in polarity from anterior to posterior electrodes (see Fig. 6B).

2.3.1.2. N300 epoch (250–350 ms). The N300 effect for this epoch appears to onset fairly early and continues on into the N400 time-window. An ANOVA examining Degree of Rotation, Repetition, Electrode Site and Hemisphere (except midline) confirmed the visual observation of a N300 effect for all three conditions with main effects of repetition (midline: F(1,23) = 23.911, p = 0.000006, $\eta_p^2 = 0.510$; medial: F(1,23) = 32.590, p = 0.000008, $\eta_p^2 = 0.586$; lateral: F(1,23) = 19.094, p = 0.0002, $\eta_p^2 = 0.454$; peripheral: F(1,23) = 9.641, p = 0.005, $\eta_p^2 = 0.295$) and an interaction of repetition × electrode site interaction (midline: F(4,92) = 14.501, p = 0.00002, $\eta_p^2 = 0.387$; medial: F(2,46) = 8.075, p = 0.004, $\eta_p^2 = 0.260$; lateral: F(3,69) = 10.870, p = 0.002, $\eta_p^2 = 0.321$; peripheral: F(4,92) = 13.665, p = 0.0002, $\eta_p^2 = 0.373$). The interaction with electrode site reflects the anterior-central distribution of this effect in each electrode column (as can be seen in the voltage maps, Fig. 6). However, none of these effects interacted with degree of rotation (Fs < 1, p > 0.1, $\eta_p^2 < 0.01$).

2.3.1.3. *N400 epoch (350–500 ms)*. In the N400 epoch, the overall comparison including all degrees of rotation showed no interactions of Degree of Rotation and Repetition, however, significant main effects of Repetition were observed (midline: F(1,23) = 56.983, p = 0.0000001, $\eta_p^2 = 0.712$; medial: F(1,23) = 73.712, p = 0.00000001, $\eta_p^2 = 0.762$; lateral: F(1,23) = 57.55, p = 0.0000001, $\eta_p^2 = 0.714$; peripheral: F(1,23) = 38.19, p = 0.000003, $\eta_p^2 = 0.624$) as well as repetition × electrode (midline: F(4,92) = 22.932,

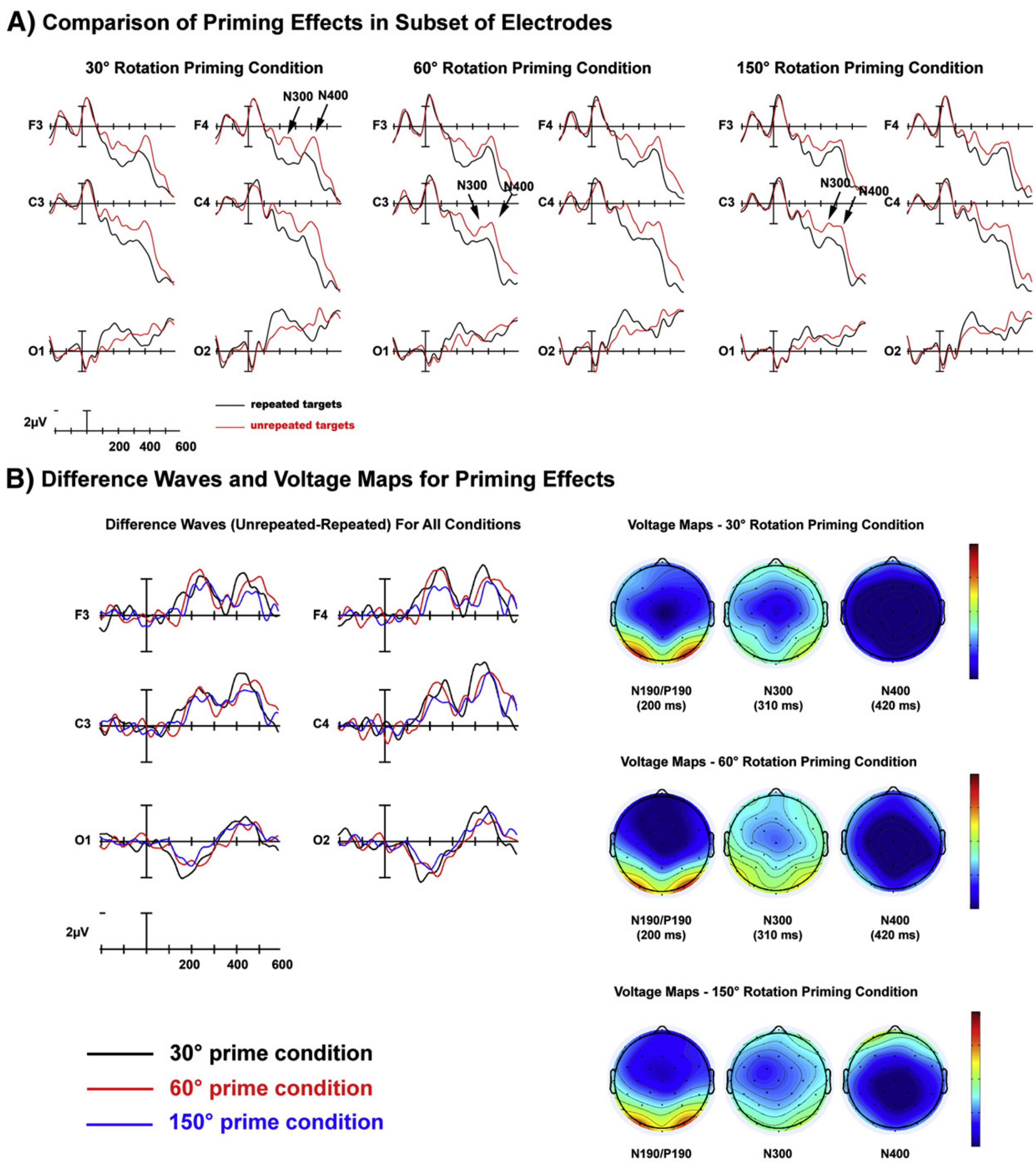

Fig. 6 – Experiment 2: (A) subset of electrodes and (B) voltage maps. Voltage maps show unrepeated – repeated voltage differences. Note that negative is plotted up.

$p=0.00000004$, $\eta_p^2=0.499$; peripheral: $F(4,92)=3.734$, $p=0.040$, $\eta_p^2=0.140$) reflecting that the repetition effect was largest over centro-parietal electrodes (see Fig. 6 — voltage maps). In addition this effect was larger in right hemisphere lateral column electrodes across all three conditions (Repetition × Electrode × Hemisphere interaction) at the lateral column ($F(3,69)=5.592$, $p=0.012$, $\eta_p^2=0.196$). Taken together an N400 effect was observed across all degrees of rotation.

2.4. *Discussion of Experiment 2*

In Experiment 1, invariant priming effects across all three ERP components were only observed for the 30° rotation condition. We hypothesized that increasing the prime exposure in Experiment 2 to 90 ms would lead to increased processing of the initial prime object and lead to invariant priming across all three of these components (N/P190, N300, N400). In particular, increased prime exposure would allow for activating an object representation that was more than merely the perceptual features of the object.

The results of Experiment 2 did indeed demonstrate invariance to rotation in depth across three different ERP components when the prime was presented for 90 ms in masked repetition priming. Priming effects for each condition were determined to be invariant to changes in viewpoint when the repetition effect (difference between repeated and unrepeated conditions for each rotation in depth) was significant for an individual condition, but also more importantly did not differ between the different rotation conditions (no Degree of Rotation × Repetition interactions). In contrast to Experiment 1, significant N300 and N400 priming effects were found for the 60° and 150° conditions.

The findings from Experiment 2 strongly suggest that the amount of exposure to the prime object determines whether an invariant or view-dependent response is observed to the target object. It is also possible that with more exposure, different features of the object are more salient and these features may be invariant to the rotations manipulated in this experiment.

3. General discussion

The findings from Experiment 1 and 2 are consistent with previous studies that have found an increase in processing with increased prime exposure, as reflected by larger amplitude ERP components (Eddy and Holcomb, 2010; Holcomb and Grainger, 2006). Manipulating view point in these two experiments extends the previous studies' findings of increased processing with longer prime exposure to ideas about the mechanisms underlying repetition effects when the stimuli are changed on some physical dimension such as viewpoint. In order to activate a representation that is invariant to this change in view-point, it appears that a sufficient amount of exposure/processing must occur. From the results of Experiment 1 it appears as though 50 ms is not enough exposure to activate a higher level form-specific/semantic representation view-invariant representation that benefits later target processing, only a viewpoint independent perceptual representation. However, as indicated by the results of Experiment 2, 90 ms does appear to be enough time to activate view-invariant representations. Therefore, somewhere between 50 and 90 ms there would appear to be a cutoff for how much information is activated for a visual representation of an object in masked repetition priming. One speculation that can be made from these findings is that a view-invariant representation can be computed sometime within this time interval and has more to do with exposure to the prime than time between the prime and target (since the SOA was held constant in these two experiments).

Our findings of N/P190 repetition effects across all manipulations are inconsistent with the previous ERP findings of Schendan and Kutas (2003), where they find the P150, an effect presumably related to the N/P190, is sensitive to object viewpoint. While the P150 and N/P190 are likely related, the former appears to rely on more long-term memory based perceptual representation whereas the N/P190 is based on the available perceptual information that is short lived from the prime that has occurred immediately prior to target presentation. The pattern of N/P190 effects is consistent with the findings of Eddy and Holcomb (2009) where manipulations of size and mirror reflection produced N/P190 repetition effects suggesting that this component shows low-level invariance to object features. However, when there was not enough overlapping perceptual information available (the condition where the stimulus was both smaller and mirror reflected from the target view) repetition effects were not observed on the N/P190 in the Eddy and Holcomb (2009) study.

The lack of N300 and 400 repetition effects in Experiment 1 is consistent with previous ERP repetition effects with mirror reflection where the earlier N/P190 effect is observed however, later N300 and N400 effects were not observed for the mirror reflected objects. The N300 and N400 repetition effects in Experiment 1 are also consistent with the findings of Epstein et al. (2008) where short repetition lags led to view-point dependent repetition suppression whereas long duration repetition of scenes led to view-point invariant repetition suppression where no recovery from adaptation was observed for different viewpoints. These findings are in contrast to Andresen et al. (2009) findings of a cost for view-point in the LOC regardless of whether long or short term adaptation was used. One caveat to consider is that neither of these studies used immediate, short-term repetition like the current studies. Their short lag was a presentation of 500 to 700 ms with an ISI of approximately 500 ms, which limits the extent to which these findings can be compared with the current experiments, but does suggest that the amount of exposure and processing time for a stimulus affects whether or not viewpoint dependent or viewpoint invariant results are found. However, there are many long term priming studies that find viewpoint dependence even with longer prime exposures (e.g., Tarr, 1995; Tarr et al., 1997). Because these studies are unmasked priming studies, it is difficult to know if top–down influences might be leading to these findings. Masked priming isolates fast feed-forward processes involved in priming and therefore, the amount of top–down influence is minimal (if any at all) and the amount of feed-forward processing of the prime determines how prior exposure to the prime influences target processing.

Grill-Spector et al. (2000) found when they used a 120 ms presentation of stimulus masked for 380 ms that 90% of the brain activation observed with a 500 ms presentation of that same stimulus was accounted for by the activation for the 120 ms presentation. However, when comparing an exposure of 40 ms to 120 ms, significantly larger effects were observed at the 120 ms. Grill-Spector et al.'s (2000) findings suggest that much of the fast feed-forward processing is occurring with brief stimulus exposures (120 ms — although, in comparison to the current paradigm, is relatively long). However, there appears to be a significant gain in the amount of processing that occurs between a 40 ms and 120 ms exposure. This is consistent with the findings in the current experiment where increasing the prime exposure from 50 ms to 90 ms led to invariant repetition priming effect. Other studies using longer exposure durations and time between exposures have found more invariant priming effects (James et al., 2002) which may point to a normalization process that takes place across a longer period of time. This is in contrast to findings from a behavioral masked repetition priming study where invariance in priming was observed regardless of prime duration (Harris et al., 2008). While they found that increasing the prime duration did lead to increased repetition priming, they found that this had no effect on the orientation dependence of priming. One explanation for these findings that conflict with the current study's results is that at different presentation durations it is possible that the outcome process (naming the object) is influenced by different representations. In Experiment 1, we did find invariance in repetition effects on the N/P190, reflecting perceptual processing, while at the longer prime duration in Experiment 2, we found invariance on both the early and later components. It is difficult to disentangle the exact processes underlying the behavioral naming effects found in the Harris et al. (2008) study although they do not necessarily need to be taken as inconsistent with the findings in the current experiments. Another possible reason for the differing findings is that our experiments involved a go–no-go categorization task, which may engage different processes than a naming task.

Overall the results of these studies demonstrate how masked repetition priming and ERPs can be used to probe the nature of object representations and how ERPs can give us precise information about the timing of when invariance is established. It appears that rather than the representation having a viewpoint dependent or invariant nature it depends upon the extent to which the representation is activated.

4. Experimental procedures

4.1. Experiment 1

4.1.1. Participants

Twenty-four volunteers (10 female, $M=19$ years old, $SD=1.2$ years), undergraduate students at Tufts University, were paid $20 to participate in this experiment. All were right-handed with normal or corrected to normal visual acuity.

4.1.2. Stimuli and procedure

Three-dimensional computer rendered models of 220 everyday objects were used in this experiment (some objects rendered in Autodesk 3ds Max 9.0; others courtesy of Michael J. Tarr, Brown University, http://www.tarrlab.org/). The objects were rotated 30°, 60°, and 150° in depth from the conventional view of the object. The most conventional view (e.g., 0° of rotation) was determined by a separate behavioral rating study completed by a different group of participants. Nineteen participants in the rating study chose the most conventional view of 12 views of an object (rotated in increments of 30°). The most conventional views (as determined by raters) were then manipulated and rendered in Autodesk to rotate the objects 30°, 60°, and 150° on the y axis (in depth) to create the conditions of interest. The objects were displayed on a white background (each 256×256 pixels) on a 19-in. display (visual angle 2°) time-locked to the vertical refresh signal of the video card (100 Hz resolution). Each subject viewed 358 pseudorandomly arranged trials composed of repeated and unrepeated prime–target pairs of objects. Repetition of items only occurred between each block and not within the blocks, with the exception of the experimental manipulation of within trial repetition of rotated objects being paired with their conventional view (we previously confirmed this does not attenuate repetition effects; e.g., we observed no repetition × block interactions in a pilot experiment). In addition, for the two experiments presented here, we did not observe any block × rotation × repetition interactions, suggesting that this repetition across block did not affect the repetition effects within each rotation condition differently.

In one condition 48 pairs of repeated objects were presented (16 in each block) where the prime was rotated 30° from the conventional view and the target was the conventional view. The second repetition condition was the same 48 items (16 different objects presented in each block), however, the prime object was rotated 60° and paired with the conventional view of that object. The third repetition condition contained the same 48 objects (16 different objects in each block) rotated 150° from the conventional view of the target. The unrepeated trials were a different set of unrepeated pairings of rotated objects in the prime position and unrelated/unrepeated conventional views of other objects in the target position. The remaining 70 trials consisted of 28 filler trials of new objects in the second and third block of the experiment. The final 42 trials contained a “probe” object (food item) paired with a nonfood object prime. All food items appeared in the target position and were either primed by a 30°, 60° or 150° rotation of a filler object from its most conventional view. Again, the 48 trials per repeated and unrepeated condition were divided among three blocks and no items repeated within a block. Items repeated across blocks with no less than 140 intervening trials. Three counterbalanced lists resulted in each repeated and unrepeated object being presented an equal number of times across participants in each of the conditions and being repeated equally between trials for repeated and unrepeated trials.

Stimuli were presented with a forward and backward mask, with a prime presented for 50 ms in between. The forward mask was presented for 300 ms and the backward mask was presented for 60 ms. The target was presented after the backward mask for 300 ms. After the target, a blank screen was presented for 1 s followed by a cue to blink which was presented for approximately 2.5 s (giving the participant enough time to blink prior to the next trial). Fig. 1 depicts examples of critical trials and their timing. Participants were instructed to attend to the screen and rapidly press a button whenever they detected an object depicting a food item. Participants were given clear instructions on what constituted a food item (e.g., live animals are not food items; food related items are not food items). All other items, including the critical items analyzed below, were viewed passively.

4.1.3. *EEG recording*

A 29-channel electrode cap (Electro-cap International) was used to collect the electroencephalogram (EEG; see Fig. 2 for electrode locations). In addition, three external electrodes were placed to monitor vertical and horizontal eye activity and differential mastoid activity. All electrodes, including one over the right mastoid, were referenced to an electrode over the left mastoid (the right mastoid was used to monitor differential left mastoid activity; none was found). Horizontal and vertical eye movements and blinks were detected from electrodes placed below and to the side of the eyes (scalp impedances of 2 kΩ). The EEG (250 Hz sampling rate, bandpass 0.01 and 40 Hz) was recorded continuously with an SA Instruments amplifier (San Diego, CA) and ERPs were averaged time-locked to the onset of targets. Trials with blinks, eye movements, and muscle artifact were rejected prior to averaging (number of trials included per condition for Experiment 1: 30° repetition condition: $M=42.6$, $SD=4.4$, 30° unrepeated condition: $M=42.8$, $SD=3.7$, 60° repetition condition: $M=43.8$, $SD=3.5$, 60° unrepeated condition: $M=43.4$, $SD=3.5$, 150° repetition condition: $M=42.8$, $SD=4.4$, 150° unrepeated condition: $M=43.1$, $SD=4.6$) and the minimum number of trials included for any one participant across conditions was 30 trials.

4.1.4. *Data analyses*

The main comparison was between repeated and unrepeated trials (the repetition effect) of objects of different degrees of rotations. Mean amplitude measurements were made in three time windows (early region N/P190 100–250 ms; N300 region 250–350 ms, and N400 region 350–500 ms). ANOVAs were performed with Degree of Rotation, Repetition, Electrode Site, and Hemisphere (except midline) as well as comparisons of repeated and unrepeated trials for each degree of rotation with the factors of Repetition, Electrode Site, and Hemisphere (except midline) as within-subject factors in four separate columnar analyses (e.g., Holcomb et al., 2005). The Geisser and Greenhouse (1959) correction was applied to all repeated measures with more than one degree of freedom.

4.2. *Experiment 2*

4.2.1. *Participants*

Twenty-four volunteers (14 female, $M=21$ years old, $SD=2.8$ years), undergraduate students at Tufts University, were paid $20 to participate in this experiment. None of these participants took part in Experiment 1. All were right-handed with normal or corrected to normal visual acuity.

4.2.2. *Stimuli and procedure*

The exact same stimuli and lists used in Experiment 1 were used in this experiment; the only changes were the duration of the prime (90 ms) and backward mask (20 ms). All of the other parameters were the same.

4.2.3. *EEG recording and data analysis*

The same recording parameters were used as in Experiment 1. Number of trials included per condition for Experiment 2: 30° repetition condition: $M=42.5$, $SD=4.5$, 30° unrepeated condition: $M=43$, $SD=4.1$, 60° repetition condition: $M=41.3$, $SD=6$, 60° unrepeated condition: $M=41.6$, $SD=5$, 150° repetition condition: $M=42.2$, $SD=5.2$, and 150° unrepeated condition: $M=42$, $SD=4.1$.

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