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Interactions between visual and semantic processing during object recognition revealed by modulatory effects of age of acquisition

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article info

abstract

The age of acquisition (AoA) of objects and their names is a powerful determinant of processing speed in adulthood, with early-acquired objects being recognized and named faster than late-acquired objects. Previous research using fMRI (Ellis et al., 2006. Traces of vocabulary acquisition in the brain: evidence from covert object naming. NeuroImage 33, 958–968) found that AoA modulated the strength of BOLD responses in both occipital and left anterior temporal cortex during object naming. We used magnetoencephalography (MEG) to explore in more detail the nature of the influence of AoA on activity in those two regions. Covert object naming recruited a network within the left hemisphere that is familiar from previous research, including visual, left occipito-temporal, anterior temporal and inferior frontal regions. Region of interest (ROI) analyses found that occipital cortex generated a rapid evoked response (~ 75–200 ms at 0–40 Hz) that peaked at 95 ms but was not modulated by AoA. That response was followed by a complex of later occipital responses that extended from ~ 300 to 850 ms and were stronger to early- than late-acquired items from ~ 325 to 675 ms at 10–20 Hz in the induced rather than the evoked component. Left anterior temporal cortex showed an evoked response that occurred significantly later than the first occipital response (~ 100–400 ms at 0–10 Hz with a peak at 191 ms) and was stronger to early- than late-acquired items from ~ 100 to 300 ms at 2–12 Hz. A later anterior temporal response from ~ 550 to 1050 ms at 5–20 Hz was not modulated by AoA. The results indicate that the initial analysis of object forms in visual cortex is not influenced by AoA. A fastforward sweep of activation from occipital and left anterior temporal cortex then results in stronger activation of semantic representations for early- than late-acquired objects. Top-down re-activation of occipital cortex by semantic representations is then greater for early than late acquired objects resulting in delayed modulation of the visual response.

Introduction

Cognitive neuroscience has taught us a great deal about the neural basis of object naming and lexical processing. The broad structure of the underlying neural networks has been identified and accompanied by analyses of the functions of the different nodes in that network and their patterns of interconnectivity (see Cattinelli et al., 2013; DiCarlo et al., 2012; Martin, 2007; Price, 2012, for reviews). At the same time, a substantial body of work in cognitive psychology and psycholinguistics has shown that some objects and words are recognized and named consistently faster and with fewer errors than others, and has explored the contribution of factors such as age of acquisition, frequency, imageability

and distinctiveness to generating those reliable differences (see Brysbaert and Cortese, 2011; Cortese and Schock, 2013; Davies et al., 2013; Juhasz, 2005). We know relatively little, however, about how such factors modulate neural processing. fMRI studies have helped to identify the brain regions whose activity levels are influenced by different properties of objects and words (e.g., Carreiras et al., 2006; de Zubicaray et al., 2012; Ellis et al., 2006; Graves et al., 2007; Zhuang et al., 2011), but exactly how and when those factors exert their influence remains poorly understood.

The present study was concerned with identifying how and when object recognition and naming are affected by age of acquisition (AoA), one of the most powerful determinants of object and lexical processing speed in adults (Alario et al., 2005; Cuetos et al., 1999; Ellis and Morrison, 1998; Juhasz, 2005; Lagonaro and Perret, 2011; Monaghan and Ellis, 2010). The benefits of early learning in object and word recognition are consistent across both participants and languages, and are

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observed over and above the contributions of other factors such as object familiarity and word frequency (Ghyselinck et al., 2004; Izura et al., 2011; Pérez, 2007). In the only previous neuroimaging study of AoA effects in object recognition, Ellis et al. (2006) presented pictures of early and late acquired objects to participants for covert naming. Functional MRI identified two regions where BOLD responses were stronger to early- than late-acquired objects − the left temporal pole and visual cortex at the occipital pole. The left anterior temporal region has been associated with the representation of concepts abstracted from perceptual and action-based experience (Patterson et al., 2007; Visser et al., 2010). The discovery of an AoA effect at this location is compatible with suggestions that early-acquired semantic representations are richer and more densely interconnected than later acquired semantic representations (Belke et al., 2005; Brysbaert et al., 2000; Steyvers and Tenenbaum, 2005). Neuropsychological studies have found that damage to anterior left temporal regions results in an impairment of object naming that is more severe for early- than late-acquired objects (Lambon Ralph et al., 1998; Woollams, 2012; Woollams et al., 2008), providing further evidence for an influence of AoA at the left temporal pole.

The observation by Ellis et al. (2006) that posterior occipital activity is also modulated by AoA during object naming was unexpected. It has, however, been argued that AoA may have effects at multiple loci within the object and word processing systems, and that one of those loci may be the perceptual analysis of visual object features (Brysbaert and Ghyselinck, 2006; Hernandez and Li, 2007; Holmes and Ellis, 2006; Johnston and Barry, 2005; Navarrete et al., 2013). For example, Catling et al. (2008) found that overlaying irrelevant contours on object pictures increased the magnitude of the AoA effect on naming speed and argued that this reflected a perceptual component in the AoA effect on object recognition (see also Catling and Johnston, 2009).

One way that AoA might come to have effects at multiple loci is if its influence lies in the way that patterns of association ("mappings") between representations develop over time. Ellis and Lambon Ralph (2000) trained an artificial (connectionist) network to associate patterns expressed across input units with patterns expressed across output units. Some pairs of associated input and output patterns ("early items") were introduced at the start of training while others ("late items") were only introduced after the network had spent some time learning the early pairs. The frequency with which early and late items were trained was varied, making it possible to demonstrate that the mature network showed an advantage for representing the early items compared with the late items that could not be explained in terms of differences in frequency of exposure but seemed to be related to changes over the course of training in the plasticity of the network. Those effects are greater when the relationships between input and output representations are arbitrary and unpredictable than when they are consistent and reliable (Lambon Ralph and Ehsan, 2006; Monaghan and Ellis, 2010). Some of the mappings between the visual features of objects and other aspects of semantic knowledge are relatively predictable. For example, animals tend to have eyes, ears, legs, rounded outlines and soft, non-shiny surfaces while man-made objects are more likely to have straight edges, sharp corners and hard, shiny surfaces. There are numerous exceptions to those generalizations, however, and some semantic knowledge does not derive predictably from visual features (e.g., Is an animal wild or domesticated? Is a berry edible or poisonous? Is a man-made object normally found inside or outside the house?). Inconsistent or unpredictable aspects of the mappings between visual features in occipital cortex and semantic knowledge in anterior temporal cortex should create the conditions required for AoA effects to arise. We note in this context that Johnston and Barry (2005) found AoA effects on reaction times (RTs) in a behavioral task that required adult participants to decide whether pictured objects were typically found inside or outside the house. The relations between objects and their names are, of course, arbitrary (Monaghan et al.,

2011), so large AoA effects would be expected in naming tasks (Alario et al., 2005; Cuetos et al., 2009; Ellis and Morrison, 1998).

Woollams (2012) found that object naming by semantic dementia patients with anterior temporal damage was influenced by both AoA and the typicality or distinctiveness of depicted objects. In a second study, naming latencies to pictured objects were measured in healthy adult participants before and after the application of repetitive transcranial magnetic stimulation (rTMS) to the left anterior temporal region. Naming latencies post-TMS showed an impact of typicality (slower to distinctive than typical objects) that was not apparent before stimulation. In contrast, the impact of AoA on naming latency after TMS was as strong as before TMS. Woollams (2012) proposed that these findings could be explained if typicality exerts its effects within the semantic representations in anterior temporal cortex (e.g., by virtue of the fact that typical concepts share more semantic features with other concepts than distinctive concepts do) while AoA effects arise in the mappings between visual and semantic representations.

Visual processing in occipital cortex and semantic processing in anterior temporal cortex can be seen as lying at opposite ends of a 'ventral stream' that is concerned with individuating and identifying objects and is distinct from a dorsal stream that is more concerned with attention and action (Goodale and Milner, 1992; Ungerleider and Mishkin, 1982; see Cloutman, in press; DiCarlo et al., 2012; Martin, 2007, for reviews). Early visual areas (V1, V2 and V3) project to area V4 which provides input to ventral processing routes that project to posterior, central and anterior temporal regions. Part of that processing involves creating visual representations that preserve object identity across transformations of position, scale, pose, etc. The ventral stream culminates in anterior temporal cortex where, according to one view, visual information is combined with inputs from other sensory modalities, along with action-based and functional knowledge, to create amodal semantic representations of objects and concepts that bring together information that is otherwise distributed around modality-specific regions of the brain (Patterson et al., 2007; Visser et al., 2010).

The present study used magnetoencephalography (MEG) to explore the modulatory effects of AoA at the occipital and anterior temporal ends of the ventral stream during object recognition and naming. As Laaksonen et al. (2012) observed, previous MEG studies of object naming have converged upon the proposal that cortical activity during object recognition and naming begins with a strong but transient occipital response (b 200 ms) which is not always reflected in the BOLD signal, possibly because of its brief duration. That short-lived occipital response is followed by more sustained responses in parietal and temporal regions (N 200 ms) and in prefrontal cortex (N 300 ms) (Hultén et al., 2009; Indefrey and Levelt, 2004; Liljeström et al., 2009; Maratos et al., 2007; Salmelin et al., 1994; Sörös et al., 2003; Vihla et al., 2006). Laaksonen et al. (2012) also noted, however, that previous MEG studies of object recognition and naming have used analysis methods sensitive only to phase-locked (evoked) responses. Laaksonen and colleagues reanalyzed three previous MEG studies of object recognition and naming (Hultén et al., 2009; Liljeström et al., 2009; Sörös et al., 2003; Vihla et al., 2006) using methods sensitive to either phase-locked responses (equivalent current dipole modeling and minimum norm estimation) or event-related modulations of spontaneous rhythmic activity (event-related Dynamic Imaging of Coherent Sources; Laaksonen et al., 2008). The analysis of evoked responses produced a similar pattern to the one noted above, with a transient response in visual cortex (b 200 ms) followed by more sustained occipital activation and a salient parietal response with activation of temporal and frontal cortices after ~300 ms. Modulation of rhythmic activity (induced responses) tended to be more long-lasting and was observed in visual and motor cortices; also in parietal and superior temporal regions. Overlap between sources of evoked responses and rhythmic activity was relatively limited, on the basis of which Laaksonen et al. (2012) concluded that evoked responses and cortical rhythms may provide complementary information about neural processing in high-level cognitive tasks.

The value of distinguishing evoked from induced activity in cognitive tasks was demonstrated by Cornelissen et al. (2009) and Wheat et al. (2010) in studies of visual word recognition. Cornelissen et al. (2009) used beamforming methods (Van Veen et al., 1997; Vrba and Robinson, 2001) to compare whole-brain responses during the recognition of written words, consonant strings and faces. "Virtual electrodes" then probed activity in the left middle occipital gyrus (MOG), the left mid fusiform gyrus (MFG) and the left and right inferior frontal gyri (IFG). Time-frequency plots were generated separately for total power changes and for the evoked (phase-locked) components of those responses. The left MOG, MFG and IFG all showed transient, phase-locked (evoked) responses that peaked significantly earlier in the MOG than in the MFG or IFG. Those transient, evoked responses were accompanied at each of the three sites by more sustained non-phase-locked (induced) responses that involved a combination of increases and decreases in power relative to baseline. Wheat et al. (2010) showed that the distinction between evoked and induced components of the neuromagnetic response at the same ROI is relevant to understanding priming effects in word recognition. Target words (for example, BRAIN) were preceded by three types of nonword prime − nonwords that sounded identical to the targets ("pseudohomophones" like brein), orthographically matched controls that did not sound identical to the targets (e.g., broin) or unrelated nonwords (e.g., lopus). Comparison of responses to pseudohomophones and orthographic controls in the left posterior IFG/precentral gyrus found a stronger response to targets following pseudohomophone than orthographic control primes around 100 ms (30−40 Hz) that was in the induced (non-phase-locked) rather than the evoked (phase-locked) component, with additional modulations between 200 and 500 ms in both the evoked and the induced components.

Clarke et al. (2011) used MEG data from a study of object naming to argue for on-line interactions between posterior visual and anterior semantic processing. Participants named pictures of objects at either a domain level (saying "living" or "manmade" in response to the pictures) or at a basic level (e.g., saying "cow" or "hammer"). Analysis of the MEG responses showed phase locking between left mid fusiform and left anterior temporal cortices that was stronger during basic- than domain-level naming from approximately 120 to 260 ms. Phase locking was also stronger between the same two regions during naming of living than nonliving things around 200 ms, and again from 300 to 340 ms. The authors proposed that object recognition involving perceptual processing in posterior occipital and fusiform cortex and semantic processing in anterior temporal cortex occurs in two stages. The first stage occurs within the first 200 ms and involves purely bottom-up, feedforward processing of visual objects that is sufficient to activate coarse-grained semantic representations in anterior temporal cortex capable of sustaining broad categorizations (such as discriminating living from nonliving things). The second stage, which may begin around 120 ms but extends to 300 ms and beyond, involves long-range, recurrent interactions between perceptual and semantic representations that are indexed by phase locking. Those recurrent interactions serve to individuate the seen objects to the point where they can be named at a basic level.

A related study by Clarke et al. (2013) took a different approach to analyzing interactions between visual and semantic regions during object naming. They investigated the effects of typicality (or distinctiveness) of objects measured in terms of the number of features an object shares with other objects (cf. Woollams, 2012). MEG responses were modulated by typicality in left ventral temporal cortex extending down to the anterior temporal pole, with stronger responses to typical than distinctive objects from 84 to 120 ms and again from 170 to 210 ms. The authors argued that recurrent interactions between visual and semantic processing are required more for the naming of objects that are hard to individuate because they share many features with other objects than for the naming of objects that share fewer features with other objects and are consequently easier to individuate.

The present experiment used MEG to probe the modulation of neuromagnetic responses by AoA during covert (silent) naming of

matched sets of early- and late-acquired objects. Participants were instructed to name the object pictures "in their heads" as quickly and as accurately as possible. The principal reason for using covert (silent) naming was that the study that formed the starting point for the present investigation used covert naming (Ellis et al., 2006) and we were keen to keep the fMRI and MEG experiments similar in that regard. When Bookheimer et al. (2005) compared overt with covert object naming, they found very similar activation patterns except in regions associated with motor activity. Some previous MEG studies of object naming have used overt naming (Clarke et al., 2011, 2013; Sörös et al., 2003; Vihla et al., 2006) while others have used passive viewing (Maratos et al., 2007), covert naming (Liljeström et al., 2009) or delayed overt naming (Hultén et al., 2009) in an effort to minimize mouth movement artifacts. Covert naming has been used in studies of visual word recognition for similar reasons (e.g., Wheat et al., 2010; Woodhead et al., 2011). Because the experimental task did not involve any overt response, a random 12% of trials were "catch trials" involving the presentation of chimeric stimuli made up from two halves of real objects. Participants were instructed to press a response button when a chimeric stimulus appeared in order to demonstrate that they were continuing to attend to the stimuli and the task. Catch trials of this sort have been involved in many previous MEG studies of silent object or word recognition (e.g., Barca et al., 2011; Cornelissen et al., 2009; Vihla et al., 2006; Wheat et al., 2010; Woodhead et al., 2011).

The experimental stimuli were pre-exposed to participants before scanning to agree the name and thereby reduce the number of occasions when a participant might generate an incorrect name covertly during the MEG task. Pre-exposure to picture stimuli has been used in other cognitive and MEG studies of object recognition to reduce error rates during scanning (e.g., Hultén et al., 2009; Levelt et al., 1998; Navarette et al., 2013; Vihla et al., 2006). In order to increase the power of the experiment, the stimuli were presented 6 times in total across six blocks of trials, with one presentation of each stimulus per block and an average of 67 trials between one presentation of a stimulus and the next. Similar repetition of sets of items across blocks of trials has been employed in EEG and MEG studies to increase statistical power (e.g., Levelt et al., 1998; Shtyrov et al., 2011). AoA effects on object naming RTs have been shown to survive pre-exposure to object stimuli (Barry et al., 2001, 2006).

A beamforming technique was employed to measure neural activity across the whole of the brain for the first 600 ms following stimulus presentation. This was done separately for three frequency bands (5−10 Hz [alpha], 10−30 Hz [beta] and 30−60 Hz [gamma]). Previous studies of word and face perception have found such subdivision of the frequency spectrum useful for capturing different aspects of perceptual and cognitive processing (Barca et al., 2011; Lee et al., 2010; Wheat et al., 2010). Virtual electrodes were then positioned at the location of peak responses in the whole-brain MEG data closest to the peaks in the occipital and anterior temporal regions where Ellis et al. (2006) found the modulation of BOLD responses by AoA. New beamformer solutions were generated for the two regions of interest and time-frequency plots computed using a longer time period (−200 to 1200 ms) and a wider range of frequencies (0−50 Hz) than the whole-brain analyses. These time-frequency plots were computed for responses to all objects (early and late combined), then separately for early and late acquired objects only, distinguishing between total and evoked power in each analysis. The separate plots were compared statistically to identify regions in the time-frequency space where the strength of the total or the evoked response at the two ROIs was significantly modulated by AoA.

Previous MEG studies of visual object recognition led us to expect a strong evoked response in occipital cortex within the first 200 ms, possibly followed by longer-lasting induced responses (Laaksonen et al., 2012). On the basis of the Ellis et al. (2006) findings we expected neuromagnetic activity in occipital cortex to be modulated by AoA (stronger to early- than late-acquired items). If the initial analysis of

the visual features of objects is influenced by AoA (Catling and Johnston, 2009; Catling et al., 2008), then the initial evoked response to visual objects might be modulated by AoA.

Semantic effects of AoA should be reflected in modulation of anterior temporal activity. Comparatively few MEG studies have reported anterior temporal responses during visual object recognition. That may reflect the fact that the strength of the MEG signal declines with distance from the sensors, making it more difficult to detect responses from relatively deep anterior temporal sources than, for example, the occipital poles (Hillebrand and Barnes, 2002). That said, Laaksonen et al. (2012) reported induced ("rhythmic") activity at both 7–12 Hz and 17–22 Hz in left superior temporal regions during overt and covert object naming that extended down to the temporal pole. Clarke et al. (2011) reported an evoked response from left medial anterior temporal cortex that was stronger during basic than domain level object naming from ~125 to 300 ms. Clarke et al. (2013) found modulation of MEG signals by distinctiveness in the left anterior temporal region from 84 to 120 ms and again from 170 to 210 ms. We also note that Bemis and Pylkkänen (2011) reported a period from ~185 to 255 ms during which MEG activity in left anterior temporal cortex was associated with combining the meanings of two words (e.g., red and boat) to decide whether or not they matched a simultaneously presented picture. Taken together, these studies indicate that it is possible to detect MEG responses originating in anterior temporal cortex and that those responses may be sensitive to semantic factors and semantic manipulations within the first 300 ms following stimulus presentation.

If the left anterior temporal lobe is a repository of amodal semantic representations (Patterson et al., 2007; Visser et al., 2010), and if AoA effects arise in the process of mapping between visual and semantic representations (Ellis and Lambon Ralph, 2000; Lambon Ralph and Ehsan, 2006; Woollams, 2012) then we would expect to see modulation of left anterior temporal activity by AoA within the first 300 ms. If the modulation of occipital activity by AoA observed by Ellis et al. (2006) is a result of top-down re-activation of visual cortex by semantic processing (Clarke et al., 2011, 2013), then the modulatory effects of AoA on occipital activity would be expected to follow the modulatory effects on anterior temporal activity.

Materials and methods

Behavioral experiment

Participants

Sixteen right-handed participants (13 females, 3 males; age range = 18–21 years) with normal or corrected-to-normal vision took part in the preliminary experiment designed to establish that the selected stimuli showed the standard effect of AoA on object naming latencies. All were native speakers of English who had spent their childhood years in the UK and were students at the University of York. Participants gave their informed consent before testing. The experimental protocol was approved by the Research Ethics and Governance Committee of the York Neuroimaging Centre, University of York, UK.

Stimuli

The experimental stimuli were colored drawings of 40 familiar objects taken from Rossion and Pourtois (2004) and based on original line drawings by Snodgrass and Vanderwart (1980). Published norms show that the 20 objects assigned to the early set can be named by 75% or more of British children aged 22–44 months while the 20 objects assigned to the late set only achieve that level of performance in children between the ages of 5 and 10 years (Morrison et al., 1997). The two sets of objects also differed on adult ratings of AoA while being matched on visual complexity, familiarity, imageability, name agreement, word length and two measures of word frequency (see Table 1). On Mann–Whitney U tests the p values for the differences between early and late sets on the matching variables were all N0.50. There were 6 living and 14 nonliving

Table 1
Characteristics of the early and late acquired stimuli.

		Early	Late
Objective age of acquisition (estimated age in months)	Mean	34.8	67.2
	SD	8.8	15.5
	Range	22–44	51–103
Rated age of acquisition (scale 1–7)	Mean	2.07	3.03
	SD	0.30	0.37
	Range	1.45–2.50	2.55–4.00
Visual complexity	Mean	2.63	2.68
	SD	0.74	0.62
	Range	1.25–3.95	1.70–3.75
Concept familiarity	Mean	3.30	3.20
	SD	0.84	0.77
	Range	1.86–4.64	2.14–4.60
Imageability	Mean	6.20	6.18
	SD	0.33	0.28
	Range	5.60–6.70	5.60–6.65
Log name frequency (Celex) (Baayen et al., 1993)	Mean	0.97	1.01
	SD	0.33	0.38
	Range	0.48–1.60	0.48–1.92
Log name frequency (WFG) (Zeno et al., 1995)	Mean	1.07	0.96
	SD	0.54	0.42
	Range	0.07–2.13	0.05–1.81
Name agreement	Mean	0.96	0.94
	SD	0.06	0.08
	Range	0.77–1.00	0.70–1.00
Name length in syllables	Mean	1.50	1.50
	SD	0.61	0.76
	Range	1–3	1–3
Name length in phonemes	Mean	4.65	4.70
	SD	1.04	1.30
	Range	3–7	3–7

Note. The object stimuli were colored versions of line drawings of familiar objects taken from Rossion and Pourtois (2004). Values for objective age of acquisition, rated age of acquisition, visual complexity, concept familiarity, imageability and name agreement were taken from Morrison et al. (1997).
Early items: banana, bell, bowl, box, button, carrot, clown, glove, jelly, jumper, leaf, peg, pencil, penguin, pram, scissors, sheep, slide, spoon, and tractor.
Late items: barrel, belt, camera, caravan, cigarette, crab, desk, dice, fridge, grapes, jug, lamp, onion, parachute, peach, plug, scales, swan, sword, and violin.

items in each set and the early and late sets covered a similar range of categories including animals, birds, fruit and vegetables, furniture, tools and modes of transport. The two sets of items are listed at the bottom of Table 1.

Procedure

The procedure for the behavioral experiment mirrored that of the subsequent MEG experiment as closely as possible. To minimize errors, the preliminary experiment began with a short training session in which participants were shown each picture accompanied by its initial and final letters separated by the appropriate number of dashes (e.g., C--A for camera) and were asked to generate the name. Each trial in the naming experiment began with a 100 ms fixation point presented in the center of a computer screen, followed by a 400 ms blank screen, after which one of the 40 object images was presented for 200 ms. There was then an interval of 2300 ms during which participants were instructed to name the object as quickly and as accurately as possible. Early and late items were randomly interleaved. Naming responses were detected by a microphone connected to a voice key. Presentation of the stimuli and measurement of naming latencies were controlled by E-Prime experiment generator software (Psychology Software Tools, version 1.1; Schneider et al., 2002).

MEG experiment

Participants

Twenty-two participants (14 females, 8 males) took part in the MEG experiment. All had normal vision or vision corrected to normal with contact lenses and had scores over 95% on the Edinburgh Handedness

Questionnaire (Oldfield, 1971). The participants were all native speakers of English who had spent their childhood years in the UK and were students at the University of York. Participants gave their informed consent before testing. The experimental protocol was approved by the Research Ethics and Governance Committee of the York Neuroimaging Centre, University of York, UK. Data from 8 participants were subsequently rejected (see below), leaving 14 participants who contributed to the final analyses (7 males, 7 females; mean age = 24.3 years, range = 20–35).

Stimuli

The experimental stimuli were the same 40 colored pictures of whole objects (20 early acquired and 20 late acquired) as were used in the behavioral experiment. Eight chimeric stimuli were created for use only in the catch trials. The 8 chimeric stimuli comprised half of one familiar object combined with half of another (e.g., half of a crocodile fused with half of a bicycle). A further 20 scrambled images were created by randomly redistributing pixels from 20 additional colored objects within a square measuring 12×12 pixels.

Procedure

The MEG experiment and associated structural MR scans were carried out in the York Neuroimaging Centre (YNiC: https://www.ynic.york.ac.uk/). Thirteen of the 14 participants had their MEG scans before their MR scans, 7 on the same day and 6 with intervals of 2 to 7 days between MEG and MR. One participant had their MR scan 5 days before their MEG scan.

The MEG experiment began with a training session in which participants were shown each picture accompanied by its initial and final letters separated by the appropriate number of dashes and were asked to generate the name (for example, saying "violin" in response to a picture of a violin and the cue V--N). The purpose of this pre-exposure to the object pictures was to ensure as far as possible that participants generated the target names correctly under the covert naming conditions of the MEG experiment. Two practice sessions then gave participants experience of the conditions of the MEG experiment using filler stimuli. This was done once outside the magnetically-shielded room and again inside the room following head digitization.

During MEG data acquisition, participants were seated with their head positioned within the helmet-shaped dewar of a 248-channel Magnes 3600 whole-head MEG scanner using SQUID magnetometers (4D Neuroimaging, San Diego, California) situated within a dimly-lit, electromagnetically-shielded room. The stimuli were back-projected onto a white screen positioned 100 cm in front of the seated participant using E-prime experiment generator software (Psychology Software Tools, version 1.1; Schneider et al., 2002) driving a Dukane 8942 ImagePro 4500 Lumens LCD projector set at the minimum brightness level to minimize the contrast between the stimulus item and the background. Each trial (epoch) began with the presentation of a central fixation cross for 100 ms followed by a 400 ms blank screen, then a stimulus (familiar, scrambled or chimeric object) for 200 ms followed by a blank screen for 2300 ms (so that each trial lasted a total of 3000 ms). The stimuli were presented at the center of the screen with an average size of approximately 7×7 cm. Participants were instructed to name the object pictures "in their heads" as quickly and as accurately as possible without moving their articulators, head or body. They were instructed to respond "pattern" silently to each of the scrambled object stimuli, and indicate the presence of one of the chimeric object stimuli (which served as 'catch trials') by pressing a button on a response box held with the index finger of their left hand. In an effort to minimize artifacts, participants were requested to blink only when the fixation cross appeared on the screen.

Six blocks of trials were presented consecutively without a break. In each block the 20 early acquired and 20 late acquired object pictures were randomly interleaved with 20 scrambled objects and 8 chimeric stimuli, making 68 trials per block. The blocks were presented in a continuous sequence without a break in between. The main experiment therefore lasted approximately 21 min. Results for the early and late acquired objects are based on $6 \times 20 = 120$ epochs per condition from each participant minus any epochs that were later rejected.

Before data acquisition, a 3-D digitizer (Polhemus 3Space® Fast track) was used to record the shape of the participant's head. Head position in the MEG system was determined through magnetic localization of five skull/scalp landmarks (coils: left and right pre-auricular, cesion, inion and the nasion). The position of the coils was recorded for each participant before and after the experiment to ensure that participant's head did not move more than 5 cm. Stabilization of the head was achieved by placing small cushions between the head and the dewar space.

Data acquisition and pre-processing

MEG data were collected in continuous mode with a sampling rate of 678.17 Hz and passband filtered between 0.1 and 200 Hz. The MEG signals were measured in a magnetically shielded room and the data were subjected to a global noise filter subtracting external, non-biological noise detected by the MEG reference channels. The data were converted into epochs lasting 3000 ms from the initial presentation of the fixation point on each trial. Individual trials were checked for the presence of major artifacts caused by eye movements, eye blinks, swallowing, false-positive push-button responses and external noise, and removed if affected.

Prior to the source space (beamformer) analysis, individual participant's MEG data was co-registered onto that participant's structural MRI scan using surface-based alignment procedure (Kozinska et al., 2001). T1-weighted MR images were obtained with a GE 3.0-T Signa Excite HDx system (General Electric, Milwaukee, USA) using an 8-channel head coil and a sagittal-isotropic 3-D fast spoiled gradient-recalled sequence. TR/TE/flip angle = 8.03 ms/3.07 ms/20°, spatial resolution of 1.13 mm $\times$ 1.13 mm $\times$ 1.0 mm, and in-plane resolution of $256 \times 256 \times 176$ contiguous slices including the entire skin surface of the head. For group analyses in source space, the individuals' data were spatially normalized to the Montreal Neurological Institute (MNI) standard brain which is based on the average of 152 individual T-1 weighted structural MR images (Collins et al., 1994). Co-registrations were visually checked and transformed manually when necessary to best fit the scalp surface.

Whole-brain beamforming

Source localization was performed using a vectorized, linearly constrained minimum-variance (LCMV) beamformer (Van Veen et al., 1997), modified as a Type 1 beamformer (Huang et al., 2004). A multisphere headmodel was used, based on local spheres fitted to the curvature of the inner surface of the skull immediately beneath each sensor. A cubic lattice of spatial filters ($5 \times 5 \times 5$ mm) was applied to the whole brain and the neural activity index was computed independently at each grid point.

Total power was compared between the 'active' (0–600 ms) and 'passive' (1400–2000 ms) time periods for the frequency bands 5–10, 10–30 and 30–60 Hz. Significance maps were generated based on the difference using a paired-sample t-statistic. Individual participant's t-maps were transformed into the standardized space defined by the MNI and superimposed on the MNI template brain with the cerebellum removed using MRIcroN software (Rorden et al., 2007; www.mricro.com).

At the second, group level of statistical analysis, a multistep procedure (Nichols and Holmes, 2004) was used to compute the permutation distribution of the maximal statistic (by re-labeling experimental conditions); in the present case the largest mean t-value (averaging across participants) from the population of virtual electrodes in standard MNI space (Nichols and Holmes, 2004; http://www.mccauslandcenter.sc.edu/mricro/mricron/main.html). For a single virtual electrode, the null hypothesis asserts that the t-distribution will be the same whatever

the labeling of experimental conditions. At the group level, for whole-brain images, the omnibus hypothesis was rejected at level $\propto = 0.05$ if the maximal statistic for the actual labeling of the experiment was in the top $100\propto\%$ of the permutation distribution for the maximal statistic. This critical value is the $(c + 1)$th largest member of the permutation distribution, where $c = [\propto N]$, $\propto N$ rounded down. This test has been shown to exert strong control over experiment-wise type I error (Holmes et al., 1996).

ROI analyses

Two ROIs were then defined. These were based on peaks in the MEG response that fell close to the two left hemisphere locations previously reported to show stronger BOLD responses to early than late acquired objects (Ellis et al., 2006). The occipital pole ROI was based on the peak for the occipital response in the 30–60 Hz band with MNI coordinates x = 8, y = −102, z = 8 in BA 17. The left anterior temporal ROI was a location x = −44, y = 22, z = −32 in BA 38 selected as the peak of left temporal pole activation in the 30–60 Hz band. This fell close to the previously-reported fMRI peak (Ellis et al., 2006) at Talairach coordinates x = −44, y = 12, z = −24 (MNI approximately x = −46, y = 12, z = −31). The MNI coordinates of the two ROIs were mapped onto individual brains using the BET tool in FSL (Jenkinson et al., 2005).

Time-frequency plots were generated at each ROI for all objects (early and late combined) then separately for early- and late-acquired objects. This was done for total power (evoked and induced responses together) and for evoked responses only from −200 to 1200 ms and from 0 to 50 Hz. Separate beamformers were used to reconstruct the time series at the two sites. Stockwell transforms (Stockwell et al., 1996) were used to compute time-frequency plots for each participant in each condition. For source reconstruction, we employed a Van Veen vectorized LCMV beamformer (Johnson et al., 2011; Van Veen et al., 1997).

Total power was computed by generating a time-frequency plot for every epoch then averaging those plots within conditions for each participant. Power changes were normalized per frequency bin with respect to the baseline. The evoked component of the response to objects was generated by averaging the virtual electrode time series across epochs to create an average time series then generating a time frequency plot of that averaged time series. Statistical comparisons were made between the time-frequency responses to early and late acquired objects for both the total and the evoked responses (Cornelissen et al., 2009; Wheat et al., 2010). These comparisons were made using PROC MIXED in SAS (SAS Institute Inc., North Carolina, US) to compute a generalized linear mixed model (GLMM). The GLMMs included repeated measures factors to account for the fact that each participant's time-frequency plot is made up of multiple time-frequency tiles. Time-frequency (spatial) variability was integrated into the models by specifying a spatial correlation model for the model residuals (Littell et al., 2006). The total and evoked components of the responses at the two ROIs were then compared statistically with a threshold of p b 0.01 (cf. Wheat et al., 2010).

Results

Behavioral experiment

Errors were removed from the analysis of reaction times (1.4%) along with responses whose RTs fell more than 2.5 SDs from the mean for each participant (4.8%). The mean latencies for correct, trimmed naming responses were significantly faster to the early acquired objects (mean latency = 550 ms) than to the late acquired objects (mean latency = 594 ms), both across participants ($t_1(14) = 4.60$, p b 0.001) and across items ($t_2(36) = 3.65$, p b 0.001). Note that these are RTs to pictures which had been pre-exposed and named once before the start of the experiment proper.

MEG experiment

Data from 8 of the original 22 participants were rejected, two because of excessive movement, one because of very strong cardiac artifacts, four because of noisy data caused by electrical/DC shifts, and one because of problems at the coregistration stage. The 14 remaining participants contributed an average of 229.6 epochs (95.7%) to the analysis of responses to the familiar objects (range = 203–238) and averaged 92% correct responses in the catch trials. Analysis concentrated on the responses to the familiar objects, focusing on the like-for-like comparison of matched sets of early- and late-acquired items. Responses to the scrambled stimuli are not reported here.

Fig. 1 shows the results of the whole-brain analysis comparing the oscillatory power of the neuronal responses during the first 600 ms post-stimulus presentation with that observed during a 'passive' baseline period when the screen was blank (1400–2000 ms post-onset). This is presented separately for 5–10 Hz (alpha), 10–30 Hz (beta) and 30–60 Hz (gamma) frequency bands. Significant increases in oscillatory power relative to the baseline (red-yellow) were observed in the 5–10 Hz frequency band at the left and right frontal poles and bilaterally at the occipital poles in the 30–60 Hz band. Significant decreases in oscillatory power (blue-green) were only observed within the left hemisphere. In the 10–30 Hz frequency band the decrease in power extended from ventral occipitotemporal (fusiform) cortex through inferior and medial lateral occipital cortex to the superior division of lateral occipital cortex. In the 30–60 Hz frequency band a decrease in power was observed at the temporal pole and at the boundary between the inferior frontal gyrus (pars opercularis) and the precentral gyrus.

Fig. 2 shows the results of the ROI analyses at the occipital and anterior temporal sites from 200 ms before stimulus onset to 1200 ms post-onset in the frequency band 0–50 Hz. The results for the occipital ROI are shown in the top row and for the anterior temporal ROI in the bottom row. The left hand panels in each row (Figs. 2A and C) show the time-frequency plots for the total response to all objects (early and late combined) at the two sites, with increases in power relative to the baseline in red-yellow and decreases in blue. The right hand panels (Figs. 2B and D) show the time-frequency plots for the evoked component of the responses. Note in relation to these plots a) that they represent new beamformer solutions based on a wider frequency band and longer time window than those that were used in generating the whole-brain analyses (Fig. 1), b) that the overall strength of the response at the occipital site was greater than at the anterior temporal site (due, at least in part, to differences in depth; Hillebrand and Barnes, 2002), and c) that the Stockwell transform used to generate the plots has better temporal resolution at higher than lower frequencies with the consequence that responses appear more spread out in time at lower than higher frequencies.

The occipital response (Fig. 2, top) showed an initial burst of evoked activity at ~75–200 ms across a wide frequency band (0–40 Hz) (Figs. 2A and B). Analysis of the peaks of this response found a mean latency of 95 ms across participants. There was a second predominantly evoked response from ~300 to 420 ms at ~10–50 Hz. Two additional responses were observed at the occipital ROI. A reduction in induced power relative to baseline (shown in blue in Fig. 2A) began at around 200 ms at ~10–25 Hz (between the two evoked responses) then continued to ~600 ms at ~5–10 Hz. That reduction in oscillatory power was followed by an increase in power from ~600 to 850 ms at ~10–25 Hz.

The neuromagnetic response at the left anterior temporal ROI (Fig. 2, bottom) was different in a number of respects. An initial burst of predominantly evoked activity occurred from ~100 to 400 ms at ~0–25 Hz (Fig. 2D). Analysis of the peaks of this response found a mean latency of 191 ms, almost 100 ms later than the initial evoked response at the occipital site. Comparison of the occipital and anterior temporal peak latencies found that the occipital peaks occurred significantly earlier in time than the anterior temporal peaks (t(13.31) = 3.48, p = 0.0039 with Satterthwaite's correction for unequal variance applied). In addition,
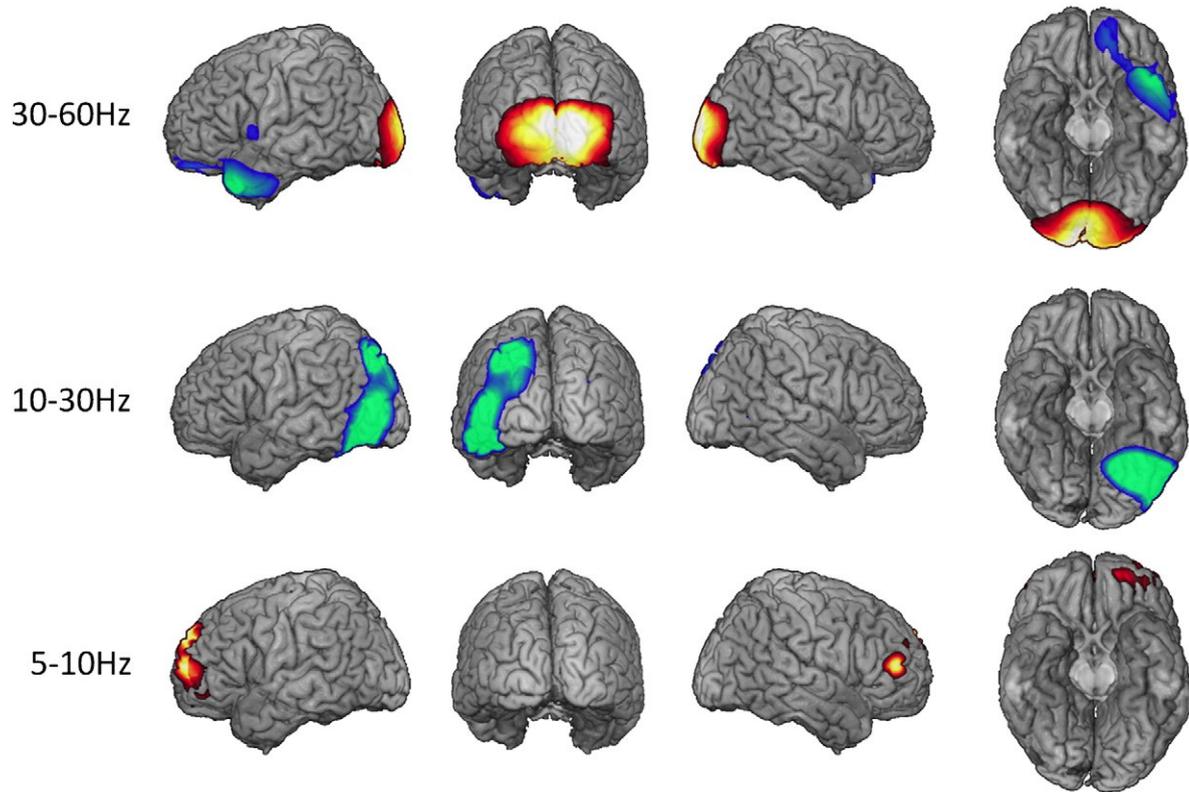
Fig. 1. Whole-brain images showing neural activity in the 5–10 Hz (alpha), 10–30 Hz (beta) and 30–60 Hz (gamma) frequency bands during an active period from 0 to 600 ms after stimulus onset compared with a baseline period of 1400–2000 ms.
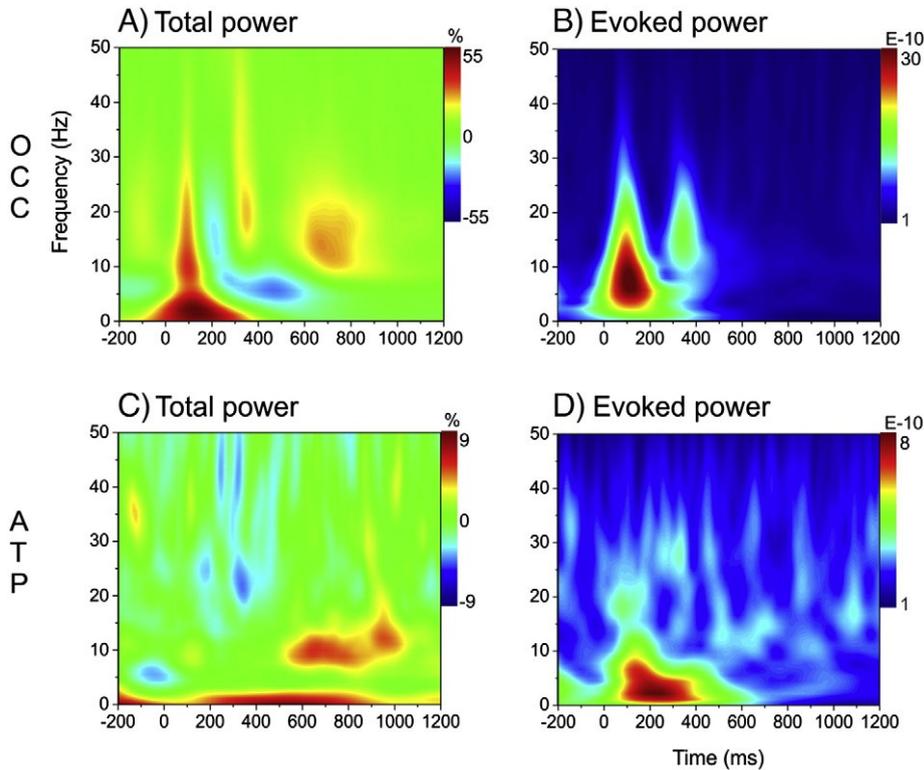

Fig. 2. ROI analyses of activity at two sites previously reported to show stronger BOLD responses to early than late acquired objects in fMRI (Ellis et al., 2006). Coordinates are based on local maxima in the whole-brain responses at 30–60 Hz (Fig. 1). Upper row shows activity from 200 ms before stimulus onset to 1000 ms post-onset in visual cortex at the occipital pole (OCC: MNI coordinates x = 8, y = −102, z = 8). Lower row shows activity at the anterior temporal pole (ATP: MNI x = −44, y = 22, z = −32). Within each row the first panels (A and C) show time–frequency plots of the total response (evoked and induced) to all objects (early and late combined) expressed as percentage change in power relative to baseline, normalized per frequency bin. Increases in power are shown in red–yellow and decreases in blue. The second panels (B and D) show time–frequency plots for the evoked (phase-locked) component of the total responses to all objects expressed as (amp × meters)^2.

the anterior temporal site showed a later, induced response that extended from ~550 to 1050 ms at ~5–20 Hz (Fig. 2C).

To investigate possible AoA effects at the two ROIs, time frequency plots for the early and late acquired objects were compared using the same time window and frequency band as in Fig. 2. These analyses involved comparing results for early- and late-acquired objects across the 6 presentations of each set. We first looked to see if MEG responses to objects at the two ROIs differed between the first and last three blocks of trials in the experiment. We computed grand average Stockwell time–frequency plots for our two ROIs across all objects (early and late combined) separately for blocks 1–3 and blocks 4–6. We used the same time period (−200–1200 ms) and the same broad frequency band (5–50 Hz) as in the other ROI analyses. The correlation between time–frequency plots computed for the first and second halves of the experiment were N0.95 at both ROIs. In other words, across all the seen objects, the results at the two ROIs were very similar indeed for the first and second halves of the experiment.

We will describe the modulation at the left anterior temporal ROI first. Fig. 3 shows the results for early- (Fig. 3A) and late-acquired (Fig. 3B) objects at the left anterior temporal site. Regions of time–frequency space in which there was significant modulation by AoA (p ᴮ 0.01) are outlined using black contours which show that the initial, evoked response in anterior temporal cortex was significantly stronger to early- than late-acquired objects from ~100 to 300 ms at ~2–12 Hz.

The modulation of the response at the occipital ROI by AoA was more complex and is shown in Fig. 4. Separate time frequency plots for early- and late-acquired objects are presented in Figs. 4A and B respectively. Regions of time–frequency space in which there were significant differences between early and late items (p ᴮ 0.01) are again outlined by black contours. Unlike the initial evoked response in anterior temporal cortex, the initial response at the occipital ROI (~75–200 ms) was not significantly modulated by AoA. Instead, modulation of the occipital response occurred from ~325 to 675 ms at ~10–20 Hz and in the induced rather than the evoked component. The area of modulation was located in the space bounded by the predominantly evoked occipital response at ~300–420 ms, the reduction in induced power from ~200 to 600 ms and the increase in induced power that occurred from ~600 to 850 ms.

To clarify the nature of this occipital modulation, Figs. 4C and D show the responses to early- and late-acquired items within the region of

time–frequency space outlined with a dashed magenta line in Figs. 4A and B that extends from 300 to 700 ms (x axes in Figs. 2C and D) and 8–24 Hz (z axes). The y axes show the strength of the response relative to baseline which is also projected down to the base of the figures as 2-D plots. Fig. 4E shows the difference between Figs. 4C and D as a 3-D surface which is again projected downwards to reveal the same difference contour as appears in Figs. 4A and B. The figures show that the neuromagnetic response in occipital cortex was stronger to early- than late-acquired objects across most of this region of time–frequency space.

Discussion

MEG analysis of visual object recognition was used to probe the modulatory effects at ROIs in occipital and left anterior temporal cortex reported by Ellis et al. (2006) to show larger BOLD responses to early- than late-acquired objects in a covert naming task. Participants seated in an MEG scanner covertly named pictures of objects that are learned either before the age of 4 years or between the ages of 5 and 10. The two sets of stimuli were matched on visual complexity, familiarity, imageability, name agreement, word length and two measures of word frequency (Table 1). Given the predominance of female participants in the preliminary experiment, we note that AoA effects have been reported to be equivalent across male and female adults (e.g., Sereno and O'Donnell, 2009).

Whole-brain images of the total response to objects revealed a network of brain areas (Fig. 1) that corresponds well to the object naming network identified in previous studies using fMRI and PET (e.g., Ellis et al., 2006; Liljeström et al., 2008; Price et al., 2005). This close degree of correspondence with the results of fMRI and PET studies may reflect the fact that Fig. 1 is based on the aggregation of responses over a relatively long period of 600 ms post-stimulus onset (cf. Cornelissen et al., 2009, Table 1). The pattern of posterior increases in oscillatory power accompanied by more anterior decreases in power is similar to that reported in MEG studies where beamforming has been applied to visual word recognition rather than object recognition (Barca et al., 2011; Cornelissen et al., 2009; Wheat et al., 2010).

The whole-brain maps included a strong, bilateral occipital response and an anterior temporal response that was lateralized to the left
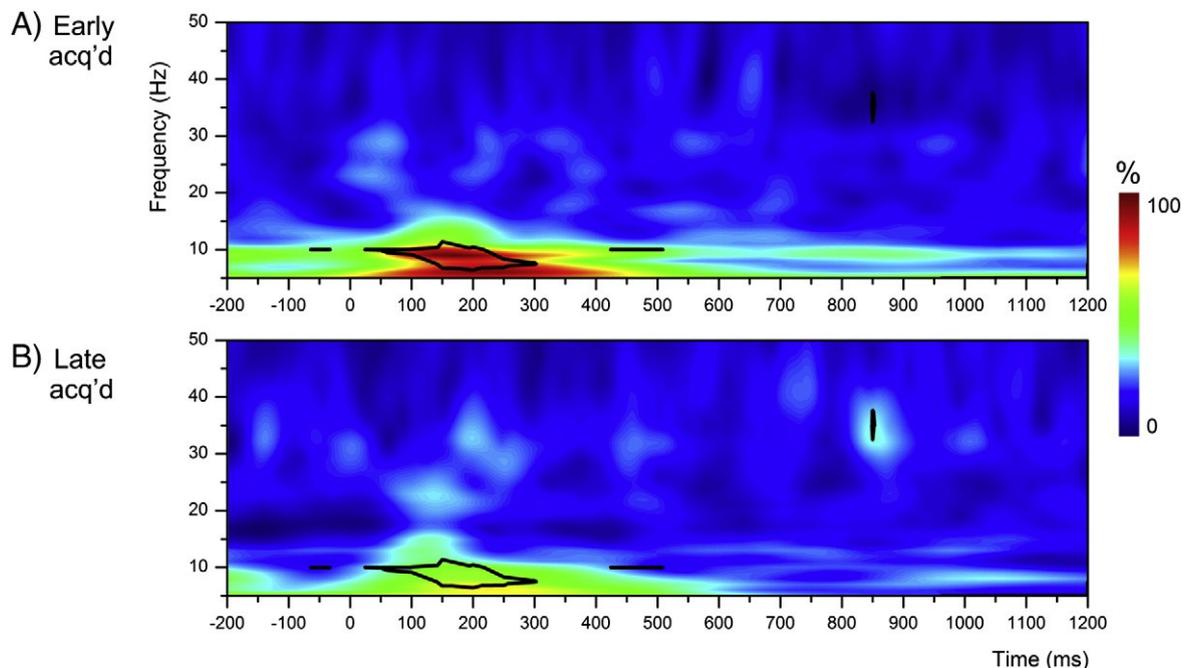

Fig. 3. Separate plots for the evoked responses to early- (3A) and late-acquired (3B) objects at the left temporal pole ROI. Areas of significant difference (p ᴮ 0.01) are enclosed by black contours (see Materials and methods).
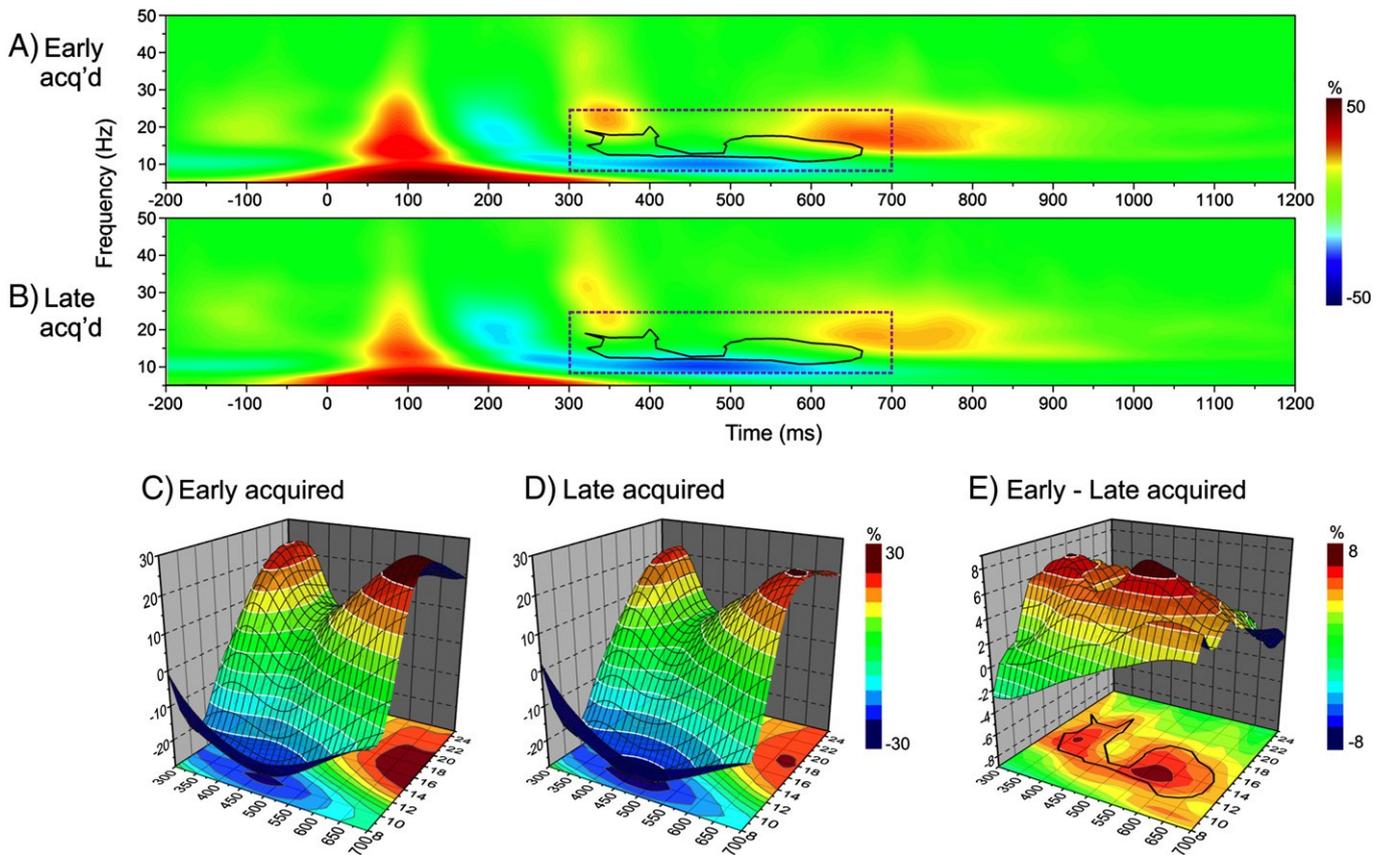
Fig. 4. Separate plots for the total responses to early- (4A) and late-acquired (4B) objects at the occipital pole ROI. Areas of significant difference (p b 0.01) are enclosed by black contours. C and D show 3D surface plots of the total response to early- and late-acquired objects respectively in the region of significant difference between conditions (300–700 ms and 8–24 Hz as indicated by the magenta dashed box in A and B). Signal strength is plotted on the z axis as percentage signal change relative to baseline for each condition. E shows the difference between the 3D surface plots in C and D. The contour showing the significant difference between conditions (as in A and B) is displayed on the 2D projection at the bottom of E.

hemisphere. Virtual electrodes were positioned at the peaks of the oc-cipital and anterior temporal responses closest to the peaks in the BOLD responses reported by Ellis et al. (2006). New time–frequency plots were generated for each ROI using a broader frequency band and a longer time period that were used to produce the whole-brain maps. (In other words, the time–frequency plots used in the ROI analyses were not based on the same beamformer solutions that generated the whole-brain images that were used to identify the coordinates for the ROI analyses.) Comparison of time–frequency plots computed separate-ly for the first and second halves of the experiment showed that the re-sults at the two ROIs were stable across the experiment (for stimuli that had been pre-exposed to participants before the start of the MEG exper-iment proper). The time–frequency plots distinguished total responses from evoked (phase-locked) responses. Induced (non-phase-locked) responses are responses that appear in the plots of total power but not in the plots showing the evoked responses. As in previous MEG studies (Laaksonen et al., 2012), a rapid and predominantly evoked re-sponse was observed in occipital cortex within the first 200 ms. That initial occipital response occurred from ~75 to 200 ms at 0–40 Hz (Figs. 2A and B), peaking at a mean of 95 ms. If AoA influenced the initial visual analysis of object features (Catling and Johnston, 2009; Catling et al., 2008), we might expect to see modulation of this evoked response by AoA, but we did not. Our results lend no support therefore to the idea that AoA affects the earliest stages of visual object identification.

An evoked response was observed at the left anterior temporal ROI from ~100 to 400 ms at ~0–25 Hz (Fig. 2D). That initial response occurred significantly later than the occipital evoked response (~100–400 ms at ~0–25 Hz with a peak at 191 ms). Anterior temporal responses during object recognition tasks have been reported in some fMRI and PET studies, particularly in studies that employed 'high level'

baseline conditions that controlled for speech processing and visual in-puts (e.g., Ellis et al., 2006; Liljeström et al., 2008; Price et al., 2005). We note that visual areas in occipital cortex are connected to anterior tem-poral cortex by the heavily-myelinated fibers of the inferior longitudinal fasciculus (Catani et al., 2003) and suggest that those fibers transmit the initial evoked response in occipital cortex to anterior temporal cortex (a distance of over 12 cm), generating an evoked response at that site around 100 ms later.

Transmitting a response from occipital to anterior temporal cortex involves mapping visual representations onto semantic representations. The connectionist accounts of Ellis and Lambon Ralph (2000), Lambon Ralph and Ehsan (2006) and Monaghan and Ellis (2010) propose that mappings of that nature are easier for associations that are established early in the course of learning than for associations that are established later. The stronger evoked response to early- than late-acquired items in left anterior temporal cortex that we observed from around 100 to 300 ms (Fig. 3) could therefore reflect those differences in ease of map-ping between different representations (cf. Woollams, 2012). An alter-native possibility is that differences in the quality and richness of early- compared with later-acquired semantic representations (Belke et al., 2005; Brysbaert et al., 2000; Steyvers and Tenenbaum, 2005) are reflected in activation of greater numbers of anterior temporal neurons and synapses, resulting in a stronger neuromagnetic response. In either case we note that the time period in which we observed modulation of the semantic response in left anterior temporal cortex by AoA overlaps with the period in which Clarke et al. (2011, 2013) reported stronger ac-tivation of medial left anterior temporal cortex by basic than domain level naming and a modulation of responses at the same site by distinc-tiveness. It also overlaps with period that Bemis and Pylkkänen (2011) associated with the process of integrating the meanings of pairs of

words. Evidence is accumulating, therefore, that semantic representations in anterior temporal cortex become active between 100 and 300 ms after stimulus onset and show influences of semantic factors. We propose that the stronger evoked response to early- than late-acquired objects in left anterior temporal cortex between 100 and 300 ms underlies the difference in the strength of the BOLD response observed at that site by Ellis et al. (2006) in their fMRI study of covert object naming. We note that in both Ellis et al. (2006) and the present data (Fig. 1), semantic response was lateralized to the left hemisphere during object naming.

We observed a delayed induced response in left anterior temporal cortex from around 550 to 1050 ms. We suggest that this could reflect activation of semantic representations by visual input along the slower cortico-cortical loops that connect either ends of the ventral stream (Catani et al., 2003). This response may reflect later semantic processing of objects but was not modulated by AoA. In contrast, delayed responses at the occipital site were modulated by AoA when the initial evoked response was not. Activity in occipital cortex was stronger to early- than to late-acquired objects from around 325 to 675 ms in the induced rather than the evoked component (Fig. 4). That period of modulation occurred within a complex of later occipital responses that began with a second predominantly evoked response from ~300 to 400 ms (Figs. 2A and B) which may represent a response to the offset of the visual stimulus which occurred at 200 ms (cf. Grützner et al., 2013; N'Diaye et al., 2004). A reduction in oscillatory power relative to baseline began in the 10–25 Hz band at around 200 ms, between the two evoked responses, and then continued to around 600 ms at 5–10 Hz (Fig. 2A). We note in relation to this response that event-related decreases in synchronized power do not necessarily reflect a decrease in neural activity: they may in fact reflect increases in more random, independent firing of neurons that serve to maximize the processing capacity of the brain areas involved (Kinsey et al., 2009; Yamagishi et al., 2005). There was a final increase in oscillatory power in occipital cortex from around 600 to 850 ms at 10–25 Hz. Occipital activity from 400 ms to 1000 ms and beyond has been reported in other MEG studies (Laaksonen et al., 2012; Vihla et al., 2006), indicating that visual cortex can remain active for an extended period after a stimulus has disappeared.

What might underlie the modulation of visual activity by AoA between around 325 and 675 ms? The fact that the modulation of visual cortex by AoA followed the modulation of left anterior temporal cortex is compatible with the view that the effect of AoA in visual cortex observed in fMRI by Ellis et al. (2006) reflects top-down re-activation of visual representations in occipital cortex by semantic representations in left anterior temporal cortex using (on this occasion) semantic-to-visual mappings that are again sensitive to AoA (cf. Clarke et al., 2011, 2013). Top-down re-activation of visual representations may serve to prolong the binding between form and meaning for stimuli that are seen only briefly (cf. Bar et al., 2006; Cardin et al., 2011; Twomey et al., 2011; Wyatte et al., 2012). This may facilitate more protracted perceptual and cognitive processing such as the processing involved in making complex semantic decisions about objects or naming object pictures with overlaid visual contours, tasks that can result in RTs in excess of 700 ms and which show influences of AoA (Catling and Johnston, 2006, 2009; Catling et al., 2008; Johnston and Barry, 2005). On the other hand, given that the mean naming latencies in the present behavioral experiment were 500 ms for early-acquired objects and 594 ms for late-acquired objects, and given that those latencies include the time required to overcome the inertia of the articulators and for the spoken name to trigger the voice key, it seems likely that effects of AoA on object naming speed observed under normal conditions (Alario et al., 2005; Cuetos et al., 1999; Ellis and Morrison, 1998; Pérez, 2007) are mediated primarily by the modulation of semantic activity in anterior temporal cortex within the first 200–300 ms.

The modulation of neuromagnetic activity by AoA at both ROIs occurred at relatively low frequencies, mainly within a broad beta band.

Beta activity is often associated with motor tasks (Davis et al., 2011) but MEG studies of visual word recognition have consistently reported activity within this frequency range (e.g., Barca et al., 2011; Cornelissen et al., 2009; Wheat et al., 2010). The beta band has been associated with long-range communication between different cortical regions (Fries, 2005; von Stein and Sarnthein, 2000), for example auditory–visual integration when participants are viewing talking faces (Fingelkurts et al., 2007) and at moments when the perception of an ambiguous visual stimulus changes from one interpretation to another (which we would interpret as reflecting fluctuating changes to the visual-to-semantic mappings; Okazaki et al., 2008). If AoA effects on object naming arise from long-range communication between visual representations in occipital cortex and semantic representations in anterior temporal cortex, it becomes less surprising that those modulations are revealed within the beta band.

A variation on the top-down re-activation account of the modulation of visual activity by AoA is based on the concept of "beta rebound" (Kilavik et al., 2013). Beta activity in sensorimotor cortex is low during the execution of a movement then shows a prominent but transient increase from 300 to 1000 ms after the movement ends. It has been suggested that this rebound is an indicator of the sensorimotor system resetting back to its resting state through active inhibition of the motor network (Gaetz and Cheyne, 2006; Pfurtscheller and Solis-Escalante, 2009). The modulation of visual activity by AoA in the present experiment began after the evoked response in visual cortex at around 300 ms, which we have suggested could be a response to the offset of the visual stimulus. The period of modulation continued through to the start of the prolonged burst of activity between 600 and 850 ms that occurred in the beta band (10–25 Hz) and may represent a beta rebound, resetting the object recognition network back to its resting state in readiness for the appearance of a new stimulus. If the binding between occipital and anterior temporal sites is modulated by AoA, resulting in stronger post-offset, top-down activation of visual representations by semantic representations for early than late items, a stronger beta rebound signal would be required to reset the network back to baseline for early than late items.

Effects of AoA on object and word recognition have been reported in studies employing EEG. Lagonaro and Perret (2011) analyzed EEG responses during the naming of early- and late-acquired objects. Differences in amplitude were observed at 120–140 ms, 220–240 ms and 320–350 ms, with larger amplitudes to early- than late-acquired items. The modulations at 120–140 ms and 220–240 ms (at least) could mirror the modulation of the rapid, evoked activation of anterior temporal by visual cortex seen in the present study. Later modulations of ERP responses by AoA (from ~300 ms to 800 ms and beyond) were observed by Cuetos et al. (2009) and Tainturier et al. (2005) during silent reading and auditory lexical decision respectively. These late modulations may be linked to delayed modulation of sensory activity generated by top-down effects. The ability of early-acquired objects to induce stronger activation at both ends of the ventral stream could also explain why neuropsychological patients whose object recognition and naming has been compromised by brain damage along the ventral stream are typically able to name early-acquired objects more successfully than late-acquired objects, even when the objects are matched in terms of factors such as familiarity and word frequency (Ellis, 2011; Holmes et al., 2006; Lambon Ralph et al., 1998; Woollams, 2012; Woollams et al., 2008). Although this has hardly been tested, the results of the present study predict that patients with semantic dementia and other conditions that compromise ventral stream processing should be better at recognizing and comprehending early-acquired objects, not just better at naming them (cf. Holmes et al., 2006).

Conclusions

Object recognition begins with a burst of evoked (phase-locked) activity within visual cortex from ~75–200 ms that peaks at around 100 ms and is assumed to reflect the encoding of the visual features of

objects (Sörös et al., 2003; Vihla et al., 2006). That response does not distinguish between objects learned early or late in life when those objects are matched on visual complexity and other factors. Activation quickly reaches left anterior temporal cortex which shows a burst of evoked activity from ~100–4000 ms, peaking around 200 ms, that is stronger for early- than late-acquired objects. The left anterior temporal lobe is assumed to be involved in storing abstract semantic representations (Patterson et al., 2007; Visser et al., 2010). We propose that the activation of this region by visual input is mediated by the direct connections provided by the heavily-myelinated fibers of the inferior longitudinal fasciculus. The modulation by AoA could reflect differences in the richness of early- and late-acquired semantic representations (Belke et al., 2005; Brysbaert et al., 2000; Steyvers and Tenenbaum, 2005) and/or differences in the quality of the mappings between visual and semantic representations created for items learned by a highly plastic system in the early stages of development compared with those created for items learned by an older, more entrenched system (Ellis and Lambon Ralph, 2000; Lambon Ralph and Ehsan, 2006; Monaghan and Ellis, 2010).

A second, predominantly evoked response in visual cortex around 300–420 ms may be a response to stimulus offset. It is followed by a decrease in induced power from ~200 to 600 ms then an increase from ~600 to 850 ms which coincided broadly with a delayed induced response from ~550 to 1050 ms at the temporal pole. Induced activity in visual cortex was stronger to early- than late-acquired objects in the beta band from ~325 to 675 ms. We have suggested two related explanations for this delayed modulation of visual activity. The first is that it reflects top-down re-activation of visual representations by semantic representations that serves to keep visual and semantic representations bound together for a period after a physical stimulus has disappeared. The second is that the delayed modulation of occipital activity by AoA reflects differences in the amount of re-setting required to return the visual system and its links to semantics to a resting state in readiness for the next stimulus.

We propose that the rapid modulation of activation in anterior temporal (semantic) cortex by AoA, and the delayed modulation of activation in visual cortex, underlie differences in the strength of the BOLD responses at those two sites observed by Ellis et al. (2006) and that the overall modulation of ventral stream responses accounts for both AoA effects on object naming speed seen in normal, healthy adults (Alario et al., 2005; Cuetos et al., 1999; Ellis and Morrison, 1998; Ghyselinck et al., 2004; Juhasz, 2005) and the superior naming of early- than late-acquired objects seen in patients with damage to ventral and anterior temporal cortex (Ellis, 2011; Lambon Ralph et al., 1998; Woollams, 2012; Woollams et al., 2008). The appearance of a mixture of evoked and induced responses at the two ROIs, and that fact that AoA modulates anterior temporal responses in the evoked component but occipital responses in the induced component, demonstrate the benefits of MEG analysis methods that are sensitive to both phase-locked and non-phase-locked responses and are capable of distinguishing between the two.

Acknowledgments

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