Greater Visual Working Memory Capacity for Visually Matched Stimuli When They Are Perceived as Meaningful

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Abstract

■ Almost all models of visual working memory—the cognitive system that holds visual information in an active state—assume it has a fixed capacity: Some models propose a limit of three to four objects, where others propose there is a fixed pool of resources for each basic visual feature. Recent findings, however, suggest that memory performance is improved for real-world objects. What supports these increases in capacity? Here, we test whether the meaningfulness of a stimulus alone influences working memory capacity while controlling for visual complexity and directly assessing the active component of working memory using EEG. Participants remembered ambiguous stimuli that could either be perceived as a face or as meaningless shapes. Participants had higher performance and increased neural delay activity when the memory display consisted of more meaningful stimuli. Critically, by asking participants whether they perceived the stimuli as a face or not, we also show that these increases in visual working memory capacity and recruitment of additional neural resources are because of the subjective perception of the stimulus and thus cannot be driven by physical properties of the stimulus. Broadly, this suggests that the capacity for active storage in visual working memory is not fixed but that more meaningful stimuli recruit additional working memory resources, allowing them to be better remembered. ■

INTRODUCTION

Visual working memory is a cognitive system used to hold visual information in an active state, protecting it from interference from new sensory inputs. The capacity of visual working memory is clearly highly limited. However, nearly all theories of visual working memory go beyond arguing capacity is limited and argue that, for a given set of stimuli, there is a "fixed" capacity, for example, a certain fixed number of objects that can be remembered regardless of complexity (e.g., of three to four objects; Awh, Barton, & Vogel, 2007), or a fixed resource pool that can be distributed among items (Bays, Catalao, & Husain, 2009). This fixed capacity is often claimed to arise from limits in attentional capacity like a certain number of attentional spotlights for maintaining items in the focus of attention (e.g., Cowan, 2005) or from more neurally inspired resource limits like a probabilistically fixed number of action potentials because of divisive normalization (e.g., Bays, 2015; Ma, Husain, & Bays, 2014). Thus, although adding new visual features, like colors in addition to orientations, may allow for parallel or object-based storage of these features in distinct neural populations and thus "more capacity" (e.g., Fougnie, Cormiea, & Alvarez, 2013), for a given set of the same stimuli—with the same objects, colors, and orientations present—capacity is argued to be fixed by many working memory models. Similarly, for sufficiently complex stimuli that already contain all of the low-level features that can be processed in parallel (orientation, color, etc.; Wolfe & Horowitz, 2017), many fixed-capacity models make the prediction that there is no longer an additional benefit from parallel storage. Instead, when each item to be remembered is more complex, each item simply requires more memory resources (e.g., Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010), resulting in worse performance at the same set size. For example, some theories say that when items become complex enough, each item requires more than one "slot" in memory (Luck, 2008).

How do these working memory limits affect memory for more realistic stimuli, like real objects, that are not just conjunctions of simple features? On the one hand, if visual working memory is best described as a set of parallel mechanisms for storing simple, low-level features and sustaining them, then realistic objects, just like very complex polygons, should simply take more of the same fixed pool of working memory resources compared to simple stimuli (as in Luria et al., 2010), because real objects tend to be more visually complex than simple features alone. On the other hand, visual working memory may not be thought of solely as reflecting the maintenance of a set of low-level visual features: Instead, perception of stimuli as meaningful may allow the recruitment of additional features and neural populations, which can be used to support working memory storage. For example, perceiving a stimulus as a face may allow the same stimulus to be

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represented in terms of not just low-level but also face-specific visual features (pose, gender, etc.), and by higher-level face regions in addition to low-level visual regions, effectively creating additional working memory capacity. This would suggest that meaningful perception of stimuli changes the nature of visual working memory capacity limits, allowing the recruitment of additional resources.

Consistent with the idea that meaningful stimuli may be better represented in visual working memory, some behavioral work has shown that familiarity and knowledge improve performance in short-term memory tasks (e.g., Zimmer & Fischer, 2020; Ngiam, Khaw, Holcombe, & Goodbourn, 2018; Brady, Konkle, & Alvarez, 2009; Curby, Glazek, & Gauthier, 2009; Jackson & Raymond, 2008; Alvarez & Cavanagh, 2004). For example, familiar faces appear to be easier to remember than unfamiliar faces (Jackson & Raymond, 2008), and familiar letters, rather than letters from unfamiliar alphabets, are more easily remembered (Ngiam et al., 2018). Such benefits can even result from moderate amounts of training (e.g., on Chinese characters: Zimmer & Fischer, 2020; Zimmer, Popp, Reith, & Krick, 2012). Such results—related to idea of "chunking"—are broadly consistent with the idea that working memory capacity is impacted by knowledge. However, it is unclear what is driving these effects on improved performance. For example, in addition to the core storage capacity of items actively in the focus of attention, it has been repeatedly found that activated forms of long-term memory that can be used for short-term storage of information (e.g., Cowan, 2005) take advantage of knowledge (e.g., long-term working memory; Ericsson & Kintsch, 1995). Thus, it is plausible that these effects of knowledge do not result from any change in "core" working memory capacity, but the recruitment of other, more passive forms of storage. For example, "chunking" has been argued to reflect some form of passive storage rather than a change in the active capacity of working memory per se (Huang & Awh, 2018), and there is some evidence for this in certain situations, where significant training with a small set of stimuli seems to allow them to be encoded in more abstract and more efficient ways (e.g., Zimmer & Fischer, 2020). In addition, some authors have claimed that differences in capacity for different stimuli result from confusability of the item pairs in the test (e.g., a decision effect), rather than a true effect on how much information can be actively maintained in working memory (Awh et al., 2007).

Some recent work has found that when people are asked to remember real-world objects (e.g., an umbrella, a chair) instead of simple isolated features (e.g., colored squares), not only is behavioral working memory capacity increased (Brady & Störmer, 2020a, 2020b; Brady, Störmer, & Alvarez, 2016), but so is a neural measure of working memory engagement (Brady et al., 2016: the contralateral delay activity [CDA]; Vogel & Machizawa, 2004). That is, people perform better and show more neural delay activity with more realistic objects, consistent with the recruitment of additional memory resources for the more realistic stimuli, rather than these items taking either more or less of the same fixed capacity or relying on alternative memory systems. However, real-world objects differ in many ways from simple isolated features: For example, they are both visually more complex and also uniquely connect to existing knowledge (i.e., are meaningful). Thus, it remains unknown what the critical factor is that allows the recruitment of additional memory resources. Furthermore, the measured neural activity during the working memory delay period (the CDA) may be sensitive to the visual complexity of stimuli independently of memory capacity per se, making it difficult to interpret changes in neural activity as being solely because of changes in working memory engagement.

Here, we test whether this neurally active component of working memory storage, measured using the CDA, is affected by the meaningfulness of a stimulus while controlling for visual complexity, that is, whether people genuinely recruit additional working memory resources for novel stimuli that can be processed in a meaningful way. We asked participants to remember two-tone images that were either perceived as meaningful or not for short periods, and measured memory performance (Experiments 1 and 2) as well as sustained neural activity during the maintenance period using electroencephalography as a direct measure of the active component of working memory (EEG; Experiment 3). Stimuli consisted of ambiguous face images ("Mooney images"; Mooney, 1957) that were carefully matched so that different images would be perceived as a face by different people (Brady, Alvarez, & Störmer, 2019; Schwiedrzik, Melloni, & Schurger, 2018); that is, the same Mooney face would be perceived as meaningful by one person but as not meaningful by someone else. Thus, among these face stimuli, there were, on average, no physical differences between images that one participant would perceive as a face or perceive as a set of black-and-white arbitrary shapes (not meaningful). In addition to these ambiguous face stimuli, we also showed participants arbitrary shapes that matched the overall low-level features of the faces (Experiments 1 and 3) or inverted versions of the faces (Experiment 2), which provided an objective non-face condition. The set of experiments allowed us to examine both the cognitive and neural consequences of visual information being perceived as meaningful or not and thus to examine whether active storage in working memory per se was changed by this perception, independent of the physical attributes of the stimulus.

EXPERIMENT 1: BEHAVIORAL CAPACITY FOR MOONEY FACES VERSUS UNRECOGNIZABLE SHAPES

Experiment 1 examined behavioral working memory capacity for Mooney faces perceived as faces versus not perceived as faces and for scrambled Mooney faces.

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Methods

Participants

All participants gave written informed consent before beginning the experiment. Experiment 1 was preregistered (aspredicted.org/blind.php?x=k8rm4k), and, in accordance with the preregistration, 24 undergraduates from the University of California, San Diego, participated for course credit (16 women, ages 18–28 years). All experiments were approved by the institutional review board of the University of California, San Diego.

Stimuli

The stimuli used consisted of 300 images (150 ambiguous Mooney faces and 150 shuffled Mooney faces that appeared as unrecognizable shapes). The ambiguous face images were previously ranked as moderately difficult to recognize a face, gaining the status "ambiguous" instead of "easy" (for details, see Brady et al., 2019; Schwiedrzik et al., 2018, which used these stimuli in a long-term memory context). This difficulty was chosen in an attempt to create a more evenly distributed subjective report of faces seen. The unrecognizable shape stimuli were created by segmenting the Mooney face images into continuous regions of white or black, labeling these as "parts," inverting each region, and then creating new images from this library of parts, subject to the constraint that no two parts of a newly generated image overlapped (Figure 1B). The target/foil images for the two-alternative forced-choice (2-AFC) test were randomly selected per trial; however, the foil image always matched the condition of the target (i.e., target: unrecognizable shapes; foil: unrecognizable shapes). To ensure that participants saw each stimulus an equal number of times and so that we could analyze item effects, each stimulus appeared 1 time as a target, 1 time as a foil, and twice as a distractor, giving a total of 300 trials per participant.

Procedure

During the experiment, participants viewed three images centered around fixation for 1000 msec (Figure 1A). We used long encoding times because of previous evidence that the role of meaningfulness may require long encoding times to become apparent (Brady & Störmer, 2020a; Brady et al., 2016). The memory display of each trial would consist of either zero, one, two, or three ambiguous Mooney faces with unrecognizable shape stimuli making up any remainder so that the memory set would always consist of three images. As such, we varied how many of these images were ambiguous face stimuli versus unrecognizable shape stimuli throughout the experiment. While the images were on the screen, participants were to maintain their eyes on the center of the screen. After the images disappeared, there was an 800-msec delay period with only image location markers on the screen. Following the delay, one of the location markers enlarged for 500 msec, indicating the location of the to-be-tested image. The target image and a foil image of the same condition (i.e., face or unrecognizable shapes) were then presented one above the other, with the space between the two images centered at the prior location marker. Participants were asked to indicate which of the two images was part of the recent set of studied images by pressing a key on the keyboard (top image: upper arrow key; bottom image: lower arrow key). The two images remained on the screen until the participant made a selection. Once the participant pressed a key, they were prompted to recall and respond with how many images they had perceived as faces during encoding (0, 1, 2, or 3) using the number pad. The experiment consisted of five blocks with 60 trials in each. The trial conditions were randomized throughout the experiment, and each trial condition was presented evenly within each block. Prior to the experiment, all participants completed two mini-blocks of four trials each as practice for the full five blocks of the experiment that followed. None of the

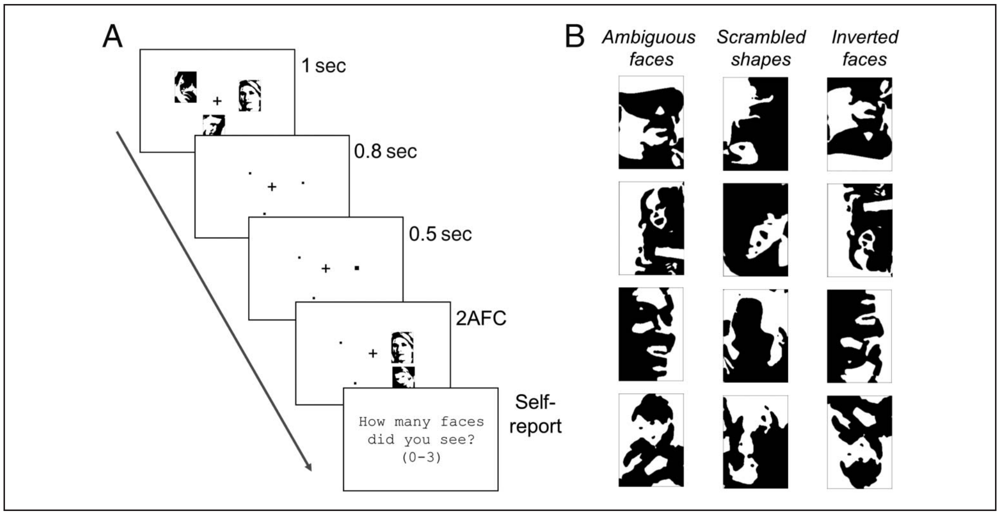

Figure 1. (A) Methods for Experiments 1 and 2. Participants saw a memory display with three images that could either be ambiguous Mooney faces or nonfaces. The nonfaces in Experiment 1 were scrambled versions of the Mooney faces ("unrecognizable shapes") and in Experiment 2 were inverted Mooney faces. After a short delay, participants were shown two images and had to indicate which one was part of the memory display (top vs. bottom). Subsequently, they were asked how many faces they perceived during encoding. (B) Example stimuli: ambiguous Mooney faces (used in all Experiments), unrecognizable shape stimuli made from scrambling Mooney images (used in Experiments 1 and 3), inverted ambiguous Mooney images (used in Experiment 2).

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images used in the practice trials were used in the full experiment.

Statistical Analyses

Experiment 1 has a within-subject, one-factor design with four levels (the number of stimuli that are upright faces, 0–3), as well as another factor, the subjectively reported number of faces seen (also 0–3). The dependent measure is accuracy in the 2-AFC memory test. As described in the preregistration, our main analysis uses a generalized linear mixed-effect model, taking all of the trials accuracy data (0/1, binomial) and fitting a model that treats both participants and items as random effects. We ask—separately and together—about the effect of the objective number of faces shown (0, 1, 2, 3) and subjective number of reported faces (0, 1, 2, 3). In particular, to look at the effect of objective number of faces alone, we examine the effect of the objective number of faces shown after taking into account random effects of participants and items:

$$\begin{aligned}&\mathit{Correct} \sim 1 + \mathit{ObjectiveFaceNum} + (1|\mathit{Item})\\&\quad + (1|\mathit{Subject})\end{aligned}$$

In a separate model, the effect of both objective and subjective number of faces and their interaction is estimated, again treating both subjects and items as random effects:

$$\begin{aligned}&\mathit{Correct} \sim 1 + \mathit{ObjectiveFaceNum} * \mathit{SubjectiveFaceNum}\\&\quad + (1|\mathit{Item}) + (1|\mathit{Subject})\end{aligned}$$

We fit these models using the fitglme function in MATLAB (The MathWorks, Inc.), with a binomial distribution. We obtained significance (p values) using MATLAB's defaults for the ANOVA function (a Type III F test). These models allow us to examine how accuracy is impacted by both the objective and subjective number of faces present, while taking into account item effects.

We also assess performance across the objectively shown number of faces with a repeated-measures ANOVA, which does not take into account the effects of individual items but may be more interpretable for readers unfamiliar with the mixed-effect approach.

Results

Participants remembered images more accurately when the memory display objectively contained more faces: Recognition accuracy increased when more faces, rather than unrecognizable shape images, were presented during the study phase, $F(3, 69) = 18.7, p < .0001$, despite the unrecognizable shapes being made from the same underlying set of shapes and correspondingly having the same low- and mid-level features present as the faces. A binomial general linear mixed-effect model showed this finding was robust not only across individuals but also after taking into account the effect of items (individual faces/unrecognizable shapes): $\beta = 0.18$, $F(1, 7198) = 34.2, p < .0001$.

Rather than focusing solely on the objective number of face stimuli present, we also analyzed the data as a function of both the objective number of faces present and the subjective number of faces participants reported perceiving. We hypothesized that faces that were present objectively would only be beneficial for memory performance when those faces were perceived by an individual, that is, an interaction between these two factors. Thus, we performed a general linear mixed-effect analysis, taking into account the random effect of individuals and items and examined the effect of both the objectively shown and subjectively reported number of faces. We found a significant effect of Number of Subjective Faces ($\beta = 0.15$, $F(1, 7196) = 4.82, p = .028$), no significant effect of the Objective Number of Faces ($\beta = -0.03$, $F(1, 7196) = 0.36, p = .55$), and an interaction between these two factors: ($\beta = 0.09$, $F(1, 7196) = 6.82, p = .009$), such that when more objective faces were shown, the subjective perception of these faces was critical to performance rather than their mere presence (Figure 2A–2B). In other words, the effect of Subjective Number of Faces seen on accuracy was larger when objectively more faces were shown. Furthermore, because items were included as random effects in the general linear mixed-effect model, we can conclude that the memory improvement was robust across the images. To further investigate whether there were reliable item effects, such that certain images were more likely to be remembered, we plotted individual performance (correct/incorrect) for each stimulus tested and did not find any reliable item effects, which further indicates there was no consistency in which images were more likely to be remembered (Figure 2C).

EXPERIMENT 2: BEHAVIORAL CAPACITY FOR MOONEY FACES VERSUS INVERTED FACES

In Experiment 1, the ambiguous faces and scrambled faces are tightly matched for visual features, as the scrambled unrecognizable shapes were made by segmenting and scrambling the set of Mooney images used in the study. However, the stimuli do differ, as the scrambling process did not perfectly preserve low- and mid-level features. Thus, in Experiment 2, to ensure that the same physical stimuli led to the same effect of recognition on memory performance, we used a different control: inverted versions of the ambiguous Mooney images. As in Experiment 1, the design and analysis plan for Experiment 2 was preregistered (aspredicted.org/blind.php?x=tt4pq2). The use of inverted images more tightly controls for image features between the recognizable and unrecognizable images since the same low- and mid-level features are present, although it also allows for the possibility that some inverted faces are recognized and/or that participants might mentally rotate the images some proportion of the time. Convergence between Experiment 1 and Experiment 2 would suggest that the

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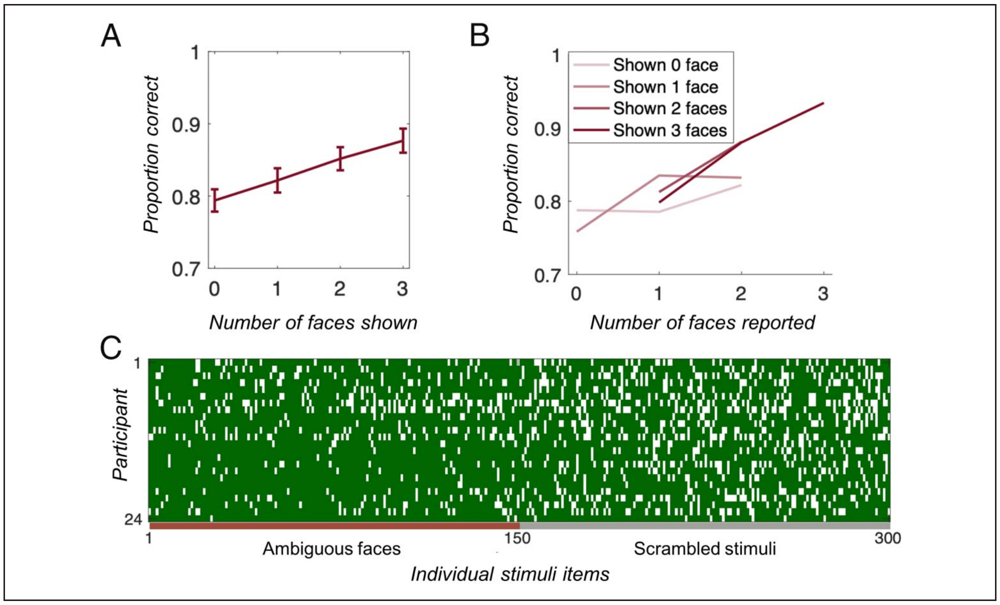

Figure 2. Results of Experiment 1. (A–B) Accuracy (proportion correct) for the 2-AFC memory match judgment depended on (A) how many faces were shown in the memory display (error bars are based on within-subject *SEM*) (B) and how many faces participants reported seeing, such that more faces perceived tended to result in better performance when more faces were shown. Given the uncertainty in both the x and y variables, the within-subject nature of the relevant comparison, and the differing number of trials at each point, no error bars capture the relevant variation in these points. However, to get a sense of the uncertainty per point, Table 1 shows the proportion of trials in each point. (C) Individual trials, where green indicates a correct response and white indicates an incorrect response. The lack of vertical columns indicates that individual items did not drive the effect, as although participants remembered faces better than scrambled images, participants were not consistent in which faces or scrambled images tended to be accurately reported.

effects we report are robust to how we choose to control for low- and mid-level features.

Methods

Participants

Experiment 2 was preregistered (aspredicted.org/blind.php?x=tt4pq2), and, in accordance with the preregistration, 24 undergraduates from the University of California, San Diego, participated, also for course credit (19 women, ages 18–32 years). One participant had performance below our preregistered exclusion criterion (average memory performance across conditions below chance) and was replaced.

Stimuli and Procedure

Experiment 2 was identical to Experiment 1 except that, rather than using scrambled Mooney faces images, it used inverted Mooney faces (Figure 1B). Thus, each trial consisted of either zero, one, two, or three upright ambiguous faces with inverted faces making up any remainder so that the memory set would always consist of three images. This more tightly controls for image features between the recognizable and unrecognizable images, although it also allows for the possibility that some inverted faces are perceived as faces and/or that participants might mentally rotate the images some proportion of the time.

Statistical Analyses

Analysis was identical to Experiment 1.

Results

Recognition accuracy increased when more faces, rather than inverted faces, were presented during the study phase, $F(3, 69) = 6.83, p = .0004$. A binomial general linear mixed-effect model showed this finding was robust not only across individuals but also after taking into account the effect of Items: $\beta = 0.11, F(1, 7198) = 14.3, p = .0002$.

To examine the effect of Subjective Perception of Faces, we again performed a general linear mixed-effect analysis taking into account the random effect of participants and items and examining the effect of both the objectively shown and subjectively reported number of faces. We found no main effect of Number of Subjective Faces (β = 0.03, $F(1, 7196) = 0.23$, $p = .63$), no main effect of the Objective Number of Faces ($\beta = -0.09$, $F(1, 7196) = 2.98, p = .08$), but an interaction between these two factors: ($\beta = 0.11, F(1, 7196) = 13.1, p = .0003$), such that, when more upright faces were shown, the subjective perception of these faces was critical to performance rather than their mere presence (Figure 3A–3B). That is, just like in Experiment 1, there was an effect of the Subjective Number of Faces reported that was larger when more faces were objectively present. In addition, looking at individual performance for each stimulus tested revealed no evidence of any reliable Item effects, which again suggests there was no consistency in which images were more likely to be remembered (Figure 3C).

Whereas Experiment 1 found a main effect of these two factors in addition to an interaction, here, we see only an interaction with no significant main effects. This arises because of a difference in how frequently people report different numbers of subjective faces, despite the same effects of both subjective and objective faces on

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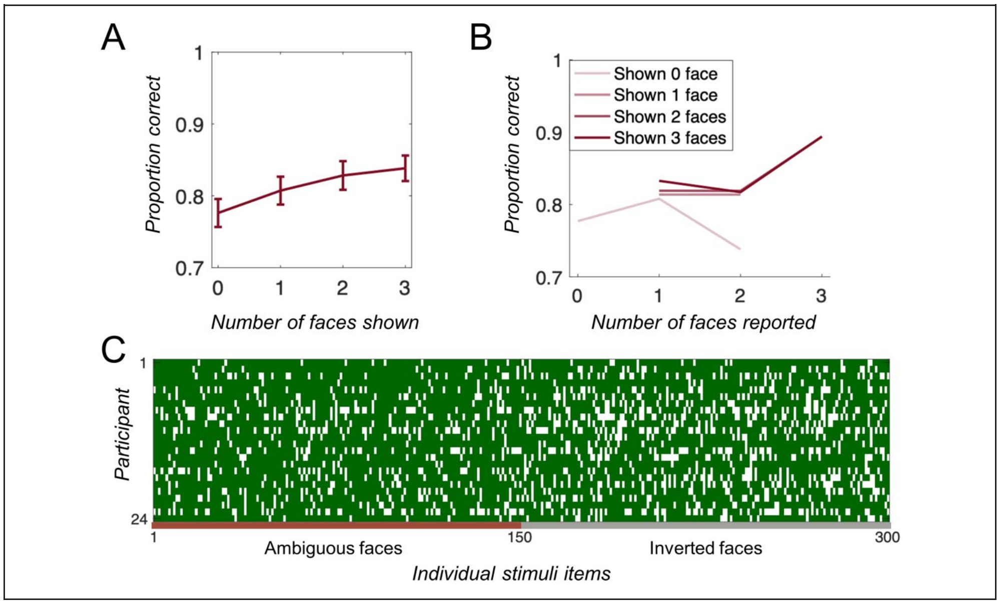

Figure 3. Results of Experiment 2. (A–B) Accuracy (proportion correct) for the 2-AFC memory match judgment depended on (A) how many faces were shown in the memory display (B) and how many faces participants reported seeing, such that more faces perceived tended to result in better performance when more faces were present. Given the uncertainty in both the *x* and *y* variables, the within-subject nature of the relevant comparison, and the differing number of trials at each point, no error bars capture the relevant variation in these points. However, to get a sense of the uncertainty per point, Table 1 shows the proportion of trials in each point. (C) Individual trials, where green indicates a correct response and white indicates an incorrect response. The lack of vertical columns indicates that individual items did not drive the effect, as although participants remembered faces better than inverted-face images, participants were not consistent in which faces or inverted-face images tended to be accurately reported.

performance in both experiments. In particular, it arises because, in Experiment 2, people saw faces more frequently in stimuli that did not have faces than they did in Experiment 1 (Table 1). Most likely, this is because inversion is just less effective than the scrambling in reducing face perception (e.g., Experiment 1, when zero face was shown, 50% of the time 0 were reported as shown; in Experiment 2, when zero face was shown, 25% of the time 0 were reported as shown). Thus, a larger proportion of trials happen to be low objective/low subjective in Experiment 1 than Experiment 2. This difference between experiments is consistent with the general advice to not interpret main effects when interactions are present: Although the effect of both objective and subjective face perception on performance appears the same in the two experiments, the significance of the main effects is different because of the different proportion of trials in each bin.

Table 1. Frequency of Total Trials Reporting Each Subjective Number of Faces for Each Objective Number of Faces for Each of the Three Experiments

Experiment 1	*Reported 0*	*Reported 1*	*Reported 2*	*Reported 3*
Shown 0	51%	32%	16%	2%
Shown 1	22%	52%	24%	3%
Shown 2	11%	31%	48%	10%
Shown 3	6%	19%	37%	39%

Experiment 2	*Reported 0*	*Reported 1*	*Reported 2*	*Reported 3*
Shown 0	24%	30%	25%	12%
Shown 1	14%	31%	41%	14%
Shown 2	9%	25%	45%	22%
Shown 3	6%	15%	40%	39%

Experiment 3	*Reported 0*	*Reported 1*	*Reported 2*	*Reported 3*
Shown 1	21%	38%	31%	10%
Shown 3	5%	25%	42%	28%

EXPERIMENT 3: ACTIVE STORAGE ASSESSED VIA THE CDA

Experiments 1 and 2 show a strong behavioral advantage not only to presenting participants with faces rather than meaningless shapes or inverted faces to remember, but with participants' own perception of those stimuli as faces. This was true even after taking into account the effects of individual items, consistent with our previous work in which we found almost no reliability in which items were perceived as faces from the same stimulus set (Brady et al., 2019). These data provide initial evidence that visual working memory performance may benefit from the perceived meaningfulness of the stimulus: When remembering an image that connects to a concept (e.g., a face), that image is remembered better than when the same visual information is not perceived as meaningful but only seen as something arbitrary (e.g., meaningless black and white shapes). This contrasts with a view where working memory capacity is fixed by the total number of items, independent of the content of those items (e.g., three to four objects regardless of complexity; Awh et al., 2007) and/or is based solely

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on the persistence of sensory information in low-level visual cortex, with images being held in a perceptual-like unprocessed state (e.g., Serences, 2016) and thus only the number of distinct low-level features being relevant to "how much" capacity is available. Instead, consistent with previous work (e.g., Ngiam et al., 2018; Brady et al., 2016; Jackson & Raymond, 2008; Alvarez & Cavanagh, 2004) but with even tighter control on stimulus features than this previous work, we find that recognized and familiar stimuli result in better behavioral performance than unrecognized or unfamiliar stimuli.

Similar effects of meaningfulness and improved memory performance have previously been found in episodic long-term memory (Brady et al., 2019; Wiseman & Neisser; 1974; Bartlett, 1932), and it has been repeatedly found that activated forms of long-term memory that can be used for short-term storage of information (e.g., Cowan, 2005) take advantage of knowledge (e.g., Ericsson & Kintsch, 1995). In addition, some authors have claimed that effects like we find here derive solely from confusability of the item pairs in the test (e.g., a decision effect), rather than a true effect of working memory maintenance (Awh et al., 2007). Thus, to test whether the increase in memory performance observed here was because of increases in active storage of information in working memory, or reflect a lack of process purity because of the use of other memory systems, such as episodic long-term memory, or a decision effect, we recorded the brain's electrophysiological responses that provide a direct measure of working memory engagement in Experiment 3.

In particular, we adapted the experiment to an EEG version of the task and showed the stimuli on a lateralized display with three images in each visual half-field, and cued participants with a central arrow to only memorize one side of the display (either left or right; Figure 4). This allowed us to measure the CDA, a neural marker of active maintenance of visual information (Vogel & Machizawa, 2004). Just like in Experiment 1, we presented ambiguous face stimuli and scrambled versions of them, but this experiment only included two conditions: one face versus three faces, to obtain a sufficient number of trials.

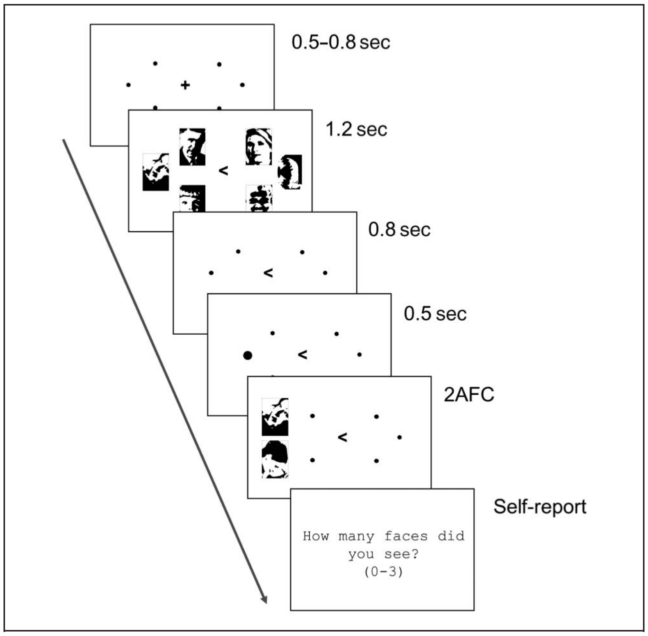

Figure 4. Methods of Experiment 3 (EEG experiment). Participants were cued to remember the items on one side of the display only (left or right). They then had to remember the three images shown on that side of the display and, then, after a delay, report which image was seen in a particular location. They then self-reported how many faces they had perceived on the to-be-remembered side of the initial display (0–3).

The CDA is a lateralized slow wave that occurs during the retention interval and tracks how much information is actively maintained (Luria, Balaban, Awh, & Vogel, 2016; Vogel, McCollough, & Machizawa, 2005), and thus can be used to infer that the information is being held actively in mind rather than stored in a passive way using a long-term memory system (Brady et al., 2016), and can distinguish between a change in how much information is maintained versus decision-level effects like confusion at test (Luria et al., 2010; Awh et al., 2007). It is often taken as an index of the focus of attention in visual working memory—for example, the active storage component of the memory system, as it has been shown to increase with the number of items participants hold in working memory (Vogel & Machizawa, 2004) and decrease when items are dropped from working memory (Williams & Woodman, 2012; Vogel et al., 2005); furthermore, the CDA correlates with the individual's working memory capacity (Störmer, Li, Heekeren, & Lindenberger, 2013; Vogel & Machizawa, 2004) and disappears when items have been consolidated into episodic long-term memory (Schurgin, Cunningham, Egeth, & Brady, 2018; Carlisle, Arita, Pardo, & Woodman, 2011). Finally, and of particular interest to this study, the CDA is not sensitive to the perceptual effort of encoding stimuli into memory or differentiating them at test, instead reflecting memory, not effort (Ikkai, McCollough, & Vogel, 2010). Thus, Experiment 3 allows us to test whether the increase in memory performance observed in Experiments 1 and 2 was because of increases in active storage of information in working memory—if it is reflected in the CDA—or whether it reflects a lack of process purity because of the use of other memory systems, such as episodic long-term memory, or reflects a decision effect rather than any memory representation change.

Methods

Participants

Twenty-three participants completed Experiment 3 and received course credit or $10 per hour for participation. Data from three participants in Experiment 3 had to be excluded because of artifacts in the EEG (> 50% of trials excluded), and data from one participant had to be excluded because part of the session was not recorded. Of the

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remaining 19 participants (13 women, ages 18–34 years) all had normal or corrected-to-normal vision.

Stimuli and Procedure

Materials and stimuli were almost identical to those used in Experiment 1. However, in Experiment 3, EEG activity was measured throughout the experiment to examine the CDA. The CDA is a lateralized slow wave that occurs during the retention interval and tracks how much information is actively maintained (Luria et al., 2016; Vogel et al., 2005). Thus, in Experiment 3, we asked whether the greater working memory capacity observed for recognizable versus unrecognizable images resulted in greater CDA as well as greater performance. If the behavioral performance increase is mirrored by a CDA increase, this would suggest that the capacity increase is mediated by greater ability to actively hold meaningful information in visual working memory—the recruitment of additional neural resources for more meaningful stimuli—rather than the use of other memory systems (like passive storage in visual long-term memory).

In order to record the lateralized CDA component, stimuli were presented on a lateralized display with three images on the left and three images on the right visual half-field, and participants were cued with a central arrow on which side to remember (Figure 4). Furthermore, to obtain a sufficient number of trials, we only included conditions in which either three ambiguous faces or one ambiguous face (and two unrecognizable shape images) was shown on each side. Because there were now six stimuli being displayed in a single study screen, the number of times each image was repeated increased. Face images were repeated ~8–9 times, and unrecognizable shape images were repeated about 4 times throughout the experiment. This was because of the trial conditions that were chosen (one-face and three-face trials). Importantly, if the participant successfully attended to one side only, the high repetition would not be overtly noticeable, because only half of the number of repetitions was on the task-relevant side of the display.

Each trial started with the presentation of six dots that served as placeholders; three were positioned on the left half of the screen in a semicircle, and the other three were presented on the right half of the screen. These dots appeared for 500–800 msec (jittered) and served as location markers for the later images. Then six images appeared on the screen as well as a central arrow cue; three images were positioned on the left half of the screen, and the other three were presented on the right half of the screen. The central arrow cue, indicating which side to memorize, appeared at the same time as the stimuli. The images were presented for 1200 msec to allow ample time to recognize the arrow cue, shift attention to the cued side covertly, and encode the images. Participants were required to maintain fixation while the images were on the screen as well as during the delay period. Therefore, participants could only use their peripheral vision to study the images on the cued side, and compliance with this was ensured by rejecting trials with horizontal eye motion from the analysis (see Electrophysiological Recordings and Analysis section). After the images disappeared, there was an 800-msec delay period with only location markers on the screen. Following the delay, one of the location markers on the cued side was enlarged and presented for 500 msec, indicating the location of the to-be-tested image. Once the test images appeared, participants were allowed to blink and move their eyes. The experiment consisted of 10 blocks with 32 trials each. The trial conditions (one vs. three faces in each study array) were randomized throughout the experiment, and each trial condition was presented evenly within each block. Prior to the experiment, all participants completed two mini-blocks of four trials each as practice for the full 10 experimental blocks that followed. None of the images used in the practice trials were used in the full experiment.

Electrophysiological Recordings and Analysis

EEG activity was recorded continuously from 32 Ag/AgCI electrodes arranged according to the 10–20 system, mounted in an elastic cap and amplified by an ActiCHamp amplifier (Brain Products GmbH). The horizontal EOG (HEOG) was acquired using a bipolar pair of electrodes positioned at the external ocular canthi, and the vertical EOG was measured at electrode FP1, located above the left eye. All scalp electrodes were referenced to an electrode on the right mastoid online. The EEG was filtered online with a cascaded integrator-comb antialiasing filter with a half-power cutoff at 130 Hz and then digitized with a 500-Hz sampling rate. Signal processing was performed with MATLAB using the EEGLAB (Delorme & Makeig, 2004) and ERPLAB toolboxes (Lopez-Calderon & Luck, 2014) and custom-written scripts. Continuous EEG data were filtered off-line with a bandpass of 0.01–112 Hz (half amplitude cutoff, with a slope of −12 dB/octave). Data were epoched into trials, and artifact rejection was performed for the interval −200 to +2000 msec relative to the memory display onset, and trials with horizontal eye movements, blinks, or excessive muscle movements were excluded from the analysis. Artifacts were detected using a semi-automated procedure, in which differences between minimum and maximum voltages were compared with a threshold value. Threshold values were determined by visual inspection for each participant individually. After using the artifact detection functions implemented in ERPLAB (Lopez-Calderon & Luck, 2014; peak-to-peak for blinks at channel FP1 and a step function to detect horizontal eye movements at the HEOG channel), we rechecked the artifact detection visually to ensure that all eye movements and blinks were detected correctly. If additional artifacts were spotted, these trials were excluded as well. For the subjects retained in the final data set (n = 19), this resulted in an average rejection rate of 18.3%.

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Artifact-free data were rereferenced to the average of the left and right mastoids, digitally low-pass filtered (half-amplitude cutoff at 30 Hz; slope of 12 dB/octave), and baselined to the 200-msec prestimulus interval. ERPs elicited by the memory display were averaged separately for each condition (one face shown, three faces shown) and were then collapsed across to-be-remembered hemifield (left, right) and hemisphere of recording (left, right) to obtain waveforms recorded contralaterally and ipsilaterally to the to-be-remembered side. Finally, because the CDA is quantified as the difference in activity across hemispheres, we calculated contralateral-minus-ipsilateral difference waveforms for each condition. For each participant, the mean CDA amplitude was measured with respect to the 200-msec prestimulus baseline at six posterior electrode sites (PO3/PO4/PO7/PO8/P7/P8) beginning 300 msec after the offset of the memory display until the test probe appeared (in this experiment, 1500- to 1950-msec post memory display onset), consistent with previous work (Brady et al., 2016; McCollough, Machizawa, & Vogel, 2007). The resulting mean amplitudes were our measure of the CDA magnitude. The exact electrode sites were chosen a priori based on a pilot participant that was not used in the main analysis. We did not use the same sites as our previous work (Brady et al., 2016) because the EEG caps used were slightly different (the previous work was done at a different university with a different system). However, to ensure that the results were not because of the specific electrodes we used, we repeated all statistical analysis using electrode sites PO3/PO4/PO7/PO8 that match our previous work (Brady et al., 2016); the relevant effects remain significant (difference in CDA amplitude between objectively shown one face versus three faces: $p = .028$; difference in CDA amplitude between subjectively reported 0/1 vs. 2/3 faces: $p = .042$).

To ensure that any lateralized effects indexed by the CDA component were not because of differences in spurious eye movements between the conditions, we compared the HEOG waveforms for remember-left versus remember-right conditions during the CDA time window, separately for the two set sizes (one face vs. three faces), and found no reliable difference for each of the left versus right comparisons, $t(18) = 1.64$, $p = .12$, for the one-face condition, and $t(18) = 1.38$, $p = .19$, for the 3-face condition. Most importantly, the left-minus-right difference waves did not differ between the conditions, $t(18) = 0.16$, $p = .87$ (see Figure 5B), demonstrating that the CDA differences we observed between conditions are not because of differences in eye movements.

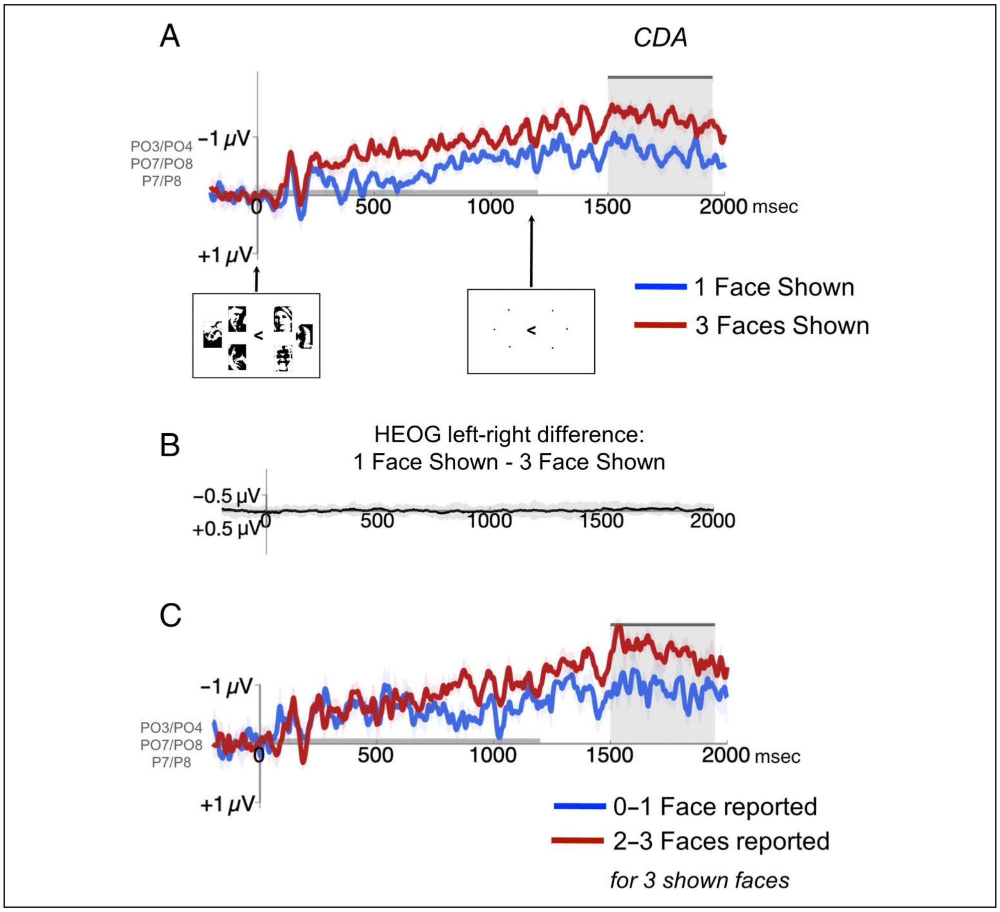

Figure 5. Results of Experiment 3. (A) Contralateral-minus-ipsilateral difference waveform over parietal-occipital electrode sites for when one face was shown (blue line) versus three faces were shown (red line). The CDA is measured 300 msec after offset of the memory display until the test probe appears (shaded gray area). Shaded areas represent within-subject standard errors of the mean at each time point. (B) We found no eye drifts that could affect the CDA magnitude differentially: As reported in the Methods section, we found no significant HEOG difference for remember-left versus remember-right trials in either condition separately. In addition, plotted here is the difference-of-differences: If small differences in left–right eye drift caused the difference in CDA between one face shown versus three faces shown, this would be reflected in a deviation from 0 in this plot, which is not present. (C) Contralateral-minus-ipsilateral difference waveform over parietal-occipital electrode sites for when three faces were shown, broken down by when zero to one face were reported (blue line) versus two to three faces were reported (red line). The CDA is measured 300 msec after offset of the memory display until the test probe appears (shaded gray area). Shaded areas represented within-subject standard errors of the mean at each time point.

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Statistical Analyses

Experiment 3 has a within-subject, one-factor design with two levels (the number of stimuli that are faces, 1 or 3) and another factor of the subjectively reported number of faces (0–3).

The behavioral dependent measure is again accuracy in the 2-AFC memory test. In addition to fitting the same generalized linear mixed-effect model from Experiments 1 and 2, the effect of the objective number of faces can now also be compared via a paired *t* test because there are only two levels.

The neural measure in Experiment 3 is the CDA. For comparing CDA based on the objective and subjective number of faces, we also rely on a linear mixed-effect model to take into account not only random effects of subjects but also items, taking advantage of the benefits of a mixed- effects analysis for electrophysiology (Bagiella, Sloan, & Heitjan, 2000). In particular, we calculate CDA on a per trial basis by: (1) first subtracting the baseline separately for each relevant electrode for each trial, (2) then subtracting contralateral electrodes from ipsilateral electrodes, and then (3) averaging over the CDA time window. Then, we fit a model that takes into account either only the objective number of faces:

$$CDA \sim 1 + ObjectiveFaceNum + (1|Item) + (1|Subject)$$

or both the objective and subjectively reported number of faces:

$$CDA \sim 1 + ObjectiveFaceNum * SubjectiveFaceNum + (1|Item) + (1|Subject)$$

We fit these models using the *fitlme* function in MATLAB, using a rank-based inverse normal transformation on CDA values (Bliss, 1967). Nearly identical results were obtained when using untransformed CDA values, but the residuals were not normally distributed, so the transformation was necessary to meet the assumptions of the statistical test. We obtained significance (p values) using MATLAB's defaults for the *anova* function (a Type III F test). In addition, to test the effect solely from the objective number of faces without controlling for item effects, we report a paired *t* test of CDA magnitude.

The main measure of the effect of objectively shown number of faces and subjectively reported number of faces is the mixed-effect model, which makes use of all participants and all trials and takes into account item effects. However, for a follow-up subjective-report analysis, we also report the effect of looking only at performance with three objective faces present, which uses only a subset of the data used in the main mixed-effect analysis but may be more interpretable for readers unfamiliar with the mixed-effect approach. To do so, we averaged ERPs according to individual's reports of how many faces they reported seeing on each trial but only included those trials on which we showed three ambiguous faces. To have a sufficient number of trials in each condition, we collapsed across reports where participants said they saw zero or one face, and two or three faces. Furthermore, for this particular analysis, we a priori restricted our EEG analysis to those participants who had a minimum of 20 trials in each bin, resulting in 14 usable participants for this analysis. On average, the remaining participants had well over 20 trials per bin, with the average number of trials per bin being 67 in these participants.

Results

In line with Experiments 1 and 2, we found that recognition accuracy increased when more faces, rather than unrecognizable shapes, were presented during the study phase, $t(18) = 2.63, p = .017$, and this was also held after taking into account the effect of items ($\beta = 0.076$, $F(1, 4964) = 4.1, p = .04$).

Importantly, this performance benefit was accompanied by increased CDA for the three- versus one-face condition, $t(18) = 2.92, p = .009$, which was also robust when taking into account the random effect of items ($\beta = .035$, $F(1, 7198) = 6.12$, $p = .01$). Thus, there is a change not only in behavioral performance, but this change is also reflected in increased CDA when more faces are shown, suggesting more information is actively held in visual working memory for faces than nonfaces.

To test to what extent the increase in working memory capacity was because of subjectively perceiving the stimuli as faces, we again looked at behavioral performance as a function of subjectively reported number of faces. We found both a main effect of Number of Subjective Faces ($\beta = 0.21$, $F(1, 4962) = 5.46, p = .019$), a main effect of the Objective Number of Faces ($\beta = 0.16$, $F(1, 4962) = 4.35, p = .037$), and, in this case, no significant interaction ($\beta = -0.07$, $F(1, 4962) = 2.7, p = .098$). This provides evidence that not only the objective number of faces shown, but also the subjective number of faces reported, drives behavioral performance.

Importantly, the effect of subjectively reported number of perceived faces was also found in the CDA data, where we observed a main effect of Number of Subjective Faces ($\beta = -0.09, F(1, 4962) = 0.23, p = .012$), no main effect of the Objective Number of Faces ($\beta = -0.04$, $F(1, 4962) = 2.98$, $p = .23$), and an interaction between these two factors ($\beta = 0.04$, $F(1, 4962) = 13.1, p = .006$), such that when more objective faces were shown, the subjective perception of these faces was critical to performance rather than their mere presence. This suggests that not only behavioral performance but also neural activity indicative of working memory storage is modulated by the subjective number of perceived faces.

Whereas this mixed-effect analysis makes use of all of the ~5000 trials of data to estimate the effect of objective and subjective number of faces, we also performed a follow-up analysis that split the data into trials where participants reported seeing zero or one face and trials where participants reported seeing two or three faces (only using

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trials in which we showed three ambiguous faces). This addresses the role of subjective perception when all three stimuli are faces. We found that performance was higher on trials where participants reported seeing more faces versus fewer faces, $t(18) = 2.83$, $p = .011$ (see Figure 6A). In addition, looking at individuals who had enough trials to analyze the magnitude of the CDA for each bin, the CDA amplitude was larger for trials where more faces were perceived during encoding compared to trials where fewer faces were seen, $t(13) = 2.35$, $p = .035$ (Figures 5 and 6B).

Table 1 reports the frequency with which trials were present in these bins, for both this experiment and Experiments 1 and 2. As expected, and consistent with this analysis, participants do not report seeing the exact number of faces that were being presented to them, allowing us to examine both the subjective perception of the stimuli as well as the objective number of faces presented.

Together, these data show that active storage in visual working memory is modulated by meaningfully perceived stimuli, with such stimuli recruiting additional storage capacity. This provides evidence against accounts where behavioral benefits for familiarity (e.g., Ngiam et al., 2018; Jackson & Raymond, 2008; Alvarez & Cavanagh, 2004) arise solely from decision-level effects like reduced confusability of stimuli at test (Awh et al., 2007), or arise solely from the recruitment of other memory systems, like visual long-term memory.

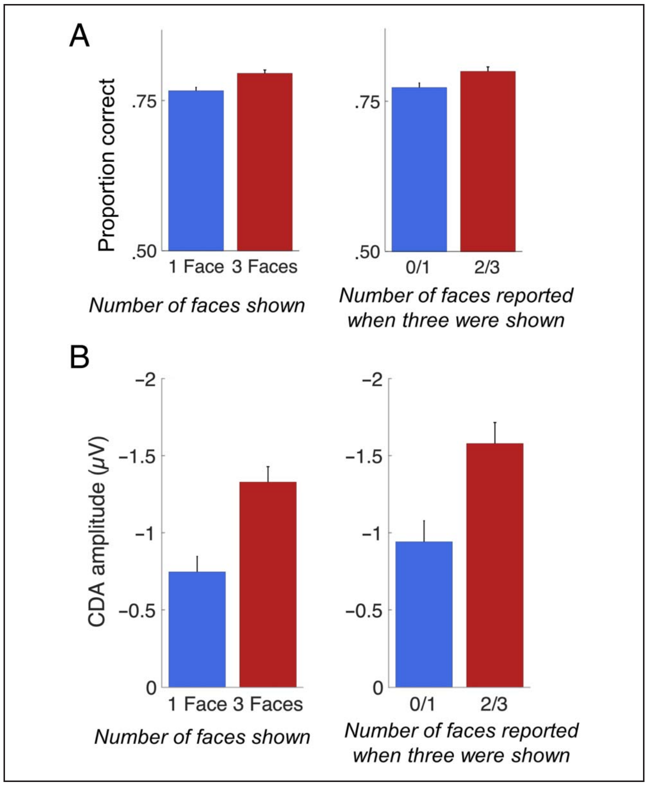

Figure 6. Results of Experiment 3. (A) Accuracy (proportion correct) for the 2-AFC memory match judgment was higher when the memory display consisted of three faces versus one face (left), and when participants reported seeing two or three faces versus zero or one face on three-face trials (right). (B) Mean CDA amplitude was higher when the memory display consisted of three faces versus one face (left), and when participants reported seeing two or three faces versus zero or one face (right).

GENERAL DISCUSSION

Together, the behavioral and EEG results suggest that visual working memory performance is heavily influenced by the type of information being stored. Specifically, we found that an observer's ability to extract meaningful information from a stimulus enables them to hold more information actively in visual working memory, even for physically identical stimuli, as the same stimulus is remembered better when it is perceived as a face than when it is not. Thus, our data suggest that visual working memory capacity is not fixed to a certain number of objects regardless of physical complexity or a globally fixed pool of resources, even for physically identical stimuli with the same orientations, spatial frequencies, and other visual information present. Instead, it critically depends on the type of information that is remembered—not how visually complex that information is, but rather whether that information can be perceived as a meaningful feature or not. Our data are broadly consistent with models where more features being present allow participants to store more information in memory (e.g., Brady et al., 2016; Wyble, Swan, & Callahan-Flintoft, 2016; Luck & Vogel, 2013), with the added idea that these additional features are not simply low-level features. Instead, additional meaningful face-level features are available for stimuli perceived as faces. In addition, our data argue against theories of visual working memory that propose that when having to remember the visual details of an object, as in the current task, persistence of sensory-like activity in low-level visual regions (e.g., V1) alone is responsible for memory performance, instead arguing for a major role for high-level interpretations of these visual details, possibly via persistence in higher-level visual areas that are selectively recruited for meaningful stimuli, such as the fusiform face area (e.g., Druzgal & D'Esposito, 2001) or via the modulation of low-level regions by high-level interpretation.

Active Storage Measured via the CDA

Active storage of information, and thus the use of working memory, is reflected in persistent neural activity in frontal and parietal brain regions (Buschman, Siegel, Roy, & Miller, 2011), and can be measured in the electroencephalogram with the CDA. The CDA is often taken as an index of the focus of attention in visual working memory—for example, the active storage component of the memory system. In particular, evidence for its selectivity to active storage in visual working memory includes the following: (1) Its magnitude increases with the number of items participants hold in working memory (Vogel & Machizawa, 2004) and decreases when items are dropped from working memory (Williams & Woodman, 2012; Vogel

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et al., 2005); (2) the CDA correlates with individual's working memory capacity (Störmer et al., 2013; Vogel & Machizawa, 2004); (3) and most importantly, the CDA disappears when items have been consolidated into episodic long-term memory (Schurgin et al., 2018; Carlisle et al., 2011). Thus, the fact that we found an increased CDA for recognizable versus unrecognizable images is consistent with the idea that the capacity increase observed behaviorally is mediated by greater ability to actively hold meaningful information in visual working memory rather than the use of other memory systems (like passive storage in visual long-term memory) or arising solely from decision-level effects like reduced confusability of stimuli at test (as proposed by Awh et al., 2007).

Our data are not consistent with an account where people have a fixed capacity in terms of the number of objects regardless of complexity (e.g., Awh et al., 2007) or other memory resources and that unrecognizable shape stimuli simply take up more of these "slots" or resources since they cannot be organized (as has sometimes been claimed about polygons and other complex stimuli; see Luria et al., 2010). This is because such an account predicts either equivalent CDA engagement in the two conditions, because, in both cases, working memory is "full" or, if anything, greater CDA in the condition with the unrecognizable shapes, as they each require multiple slots or greater resource usage in memory. Instead, we find that the face stimuli not only result in better performance but also greater sustained neural activity as measured by the CDA, suggesting the recruitment of additional memory resources for the meaningful stimuli. This is in direct contrast to the predictions of fixed capacity accounts of visual working memory, which argue that only additional low-level features can be used to recruit additional capacity. Thus, our data provide evidence that meaningfulness—rather than the visual information on our retinas—underlies visual working memory capacity.

In the current work, we test only set size 3. It is possible that testing different set sizes would reveal a difference between "how many" items are remembered versus "how accurately" each is perceived/remembered, with meaningfulness having a differential impact on such factors. We believe the current evidence from both fitting continuous report data (e.g., Schurgin, Wixted, & Brady, 2020; Bays, 2015; Van den Berg, Shin, Chou, George, & Ma, 2012) and from receiver operating characteristic analysis (Robinson, Benjamin, & Irwin, 2020) strongly favors a view where items simply vary continuously in how much noise they are encoded with or how much noise is accumulated during the delay, rather than a view where a large fraction of items that were seen 1 sec ago are completely lost as though they had never been seen. Because the most up-to-date frameworks do not feature all-or-none forgetting of items from memory, and thus reject this distinction between "how many" and "how precisely" items are remembered, we do not focus on it here: Instead, we emphasize only that additional memory capacity can be recruited for meaningful stimuli.

Our finding of increased active storage for more meaningful stimuli differs from other studies that found increased behavioral performance for familiar relative to unfamiliar stimuli, similar to our behavioral effects, but did not observe an increase in neural delay activity for the familiar stimuli. For example, when Zimmer et al. (2012) and Zimmer and Fischer (2020) trained participants on a subset of Chinese characters, they showed higher behavioral performance in a working memory task for these learned stimuli, but *less* neural delay activity for the familiar characters relative to unfamiliar characters, at least at low set sizes. Zimmer et al. suggested that memory for familiar characters was supported by long-term memories acquired during training (e.g., word form acquisition; Zimmer & Fischer, 2020; Zimmer et al., 2012)—effectively, people had learned abstract labels for the characters, which could be used to support performance in the working memory task with less stimulus-specific information needing to be encoded. This is broadly consistent with our suggestion about the role of active storage in working memory: In our study, the stimuli were generally novel, and perceiving a face in the stimulus allowed participants to encode additional stimulus-specific information (e.g., face-specific features) that could help support memory, resulting in increased delay activity. By contrast, in the Zimmer et al. work, because the stimuli were well learned, fewer features needed to be encoded to support memory for the learned stimuli—a simple label (verbal or conceptual) is sufficient to remember them—and so participants did not store as many specific visual features to succeed at the task, resulting in reduced delay activity.

Subjective and Objective Effects

In the current work, we show evidence for two effects: We show that subjective perception modulates how accurately Mooney faces are remembered, and we show that the objective status of the image as a face or not (either scrambled or inverted) also modulates how accurately these images are remembered. This provides converging evidence that it is truly the perception of the stimuli as meaningful that is relevant both for behavioral performance and for increased working memory-related neural activity. In particular, neither analysis, taken alone, controls for all possible alternative accounts: For example, the analysis conditioning on the subjectively reported number of faces is inherently correlational. Thus, in theory, prestimulus states could modulate both how many faces participants report and how well they perform in the memory task. In addition, small differences in low-level features or mid-level features could, in theory, account for the objective face effect. However, taken together, the two results support our main conclusion that seeing something as a face results in higher memory capacity, given that we find the same effect when we show participants objectively more faces, a causal experimental manipulation, and in participants' subjective reporting of their experience.

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Differential Attention to Faces

Might the benefit of face perception to memory in these studies arise in part because people are more interested in faces, and so differentially attend to faces within a trial? This cannot straightforwardly account for the benefit to overall performance of more faces being present, that is because our conditions do not refer to trials where a "face" was probed versus not probed (which could be affected by differential attention), but instead to average performance for a random item from the entire display, regardless of which item was probed—so if nonfaces were impaired but faces helped by the allocation of resources, but the same overall pool of resources was used, this would average out and result in no overall benefit or cost.

Our data can also be used to test this account directly: A differential attention account predicts that, as more faces are present and/or perceived, performance on trials where nonfaces are probed will drop by a large amount, as people preferentially encode the faces. We do not see any evidence for this in our data. Sorting by objective number of faces, in Experiment 1, we find performance on nonface trials is 79% with zero face present, 77% with one face present, and 78% with two faces present. In Experiment 2, performance on nonface trials is 78% with zero face present, 77% with one present, and 76% with two faces present. Fitting a mixed-effect model that accounts for subject and item effects to only data from trials where a nonface is probed also reveals no effect of the number of objective or subjective faces on performance and no interaction (all $p > .10$ in both experiments). Thus, we see no evidence that our effects are driven by differential attention to faces at the cost of nonfaces, within the same pool of resources—instead, our data show that participants simply remember face stimuli better than nonface stimuli regardless of how many of each are present, consistent with our interpretation that perceiving a stimulus as a face allows the use of face-specific features and, correspondingly, the recruitment of additional working capacity.

Knowledge and Visual Working Memory

The observed benefits for working memory performance from perceived faces and for remembering real-world objects (Brady & Störmer, 2020a, 2020b; Brady et al., 2016) suggest that meaningful processing is the critical attribute that gives rise to enhanced active storage, similar to the role of meaning in long-term memory (Konkle, Brady, Alvarez, & Oliva, 2010; McWeeny, Young, Hay, & Ellis, 1987; Bower, Karlin, & Dueck, 1975). What determines the meaningfulness of an object? The present findings show that when a visual stimulus is associated with a high-level object category (i.e., a face), this can be sufficient to increase working memory performance. This suggests that high-level visual templates such as knowing what a face looks like can provide a link to connect an incoming stimulus to existing knowledge and familiar categories. In this case, meaningfulness may mostly depend on high-level visually derived categories, but in other cases, for example, real-world objects, it seems plausible that other, even richer conceptual associations are being activated to induce meaningfulness. Such perception may allow the engagement of more high-level brain regions, allowing people to maintain neural activity over the delay not only in low-level sensory areas but also in high-level regions relevant to the processing of the stimulus, which may be higher-level visual regions, or other brain regions activated by semantic knowledge. For example, fMRI studies have shown that when participants remember faces, the fusiform face area is activated (Salmela, Ölander, Muukkonen, & Bays, 2019; Druzgal & D'Esposito, 2001), and when participants remember images of hands, somatosensory regions are recruited (Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018). Another recent study showed that meaningful rather than perceptually matched but nonmeaningful stimuli results in greater activity in the ventral stream during visual working memory tasks (Stojanoski, Emrich, & Cusack, 2019), again consistent with the idea that stimuli that connect to knowledge are represented in other, additional higher-level visual areas during working memory tasks. Thus, it is possible that, in some sense, the improved capacity we observe arises even during perception (or encoding) of the stimuli: Recruitment of higher-level regions while viewing the stimuli provides the foundation for these regions to play a role in working memory.

Consistent with this, we recently showed that how stimuli are processed during encoding is critical in determining whether benefits for meaningful and real-world objects arise (Brady & Störmer, 2020a). In a series of experiments, we demonstrate that sequential encoding of real-world objects—where each stimulus is shown one at a time, thus allowing focused and item-based encoding—results in larger object benefits relative to simultaneous encoding of all stimuli at once, as often done in working memory studies (and as done here). We believe that sequential encoding is one particularly effective way to ensure that participants recognize an individual item's identity, can connect it to existing knowledge, and therefore recruit additional neural resources to hold that item in memory. Another way such deep encoding of stimuli can be achieved is by using long encoding times, as we have done here and in other studies (Brady & Störmer, 2020b; Brady et al., 2016); however, it seems that long encoding times are not always sufficient in eliciting a benefit for meaningful objects (Li, Xiong, Theeuwes, & Wang, 2020; Quirk, Adam, & Vogel, 2020; but see Brady & Störmer, 2020b, for an alternative explanation for these differences), suggesting that variation in how participants encode a particular memory display is an important consideration when studying memory for meaningful stimuli. In this study, for example, participants were encouraged to try to connect the memory stimuli to knowledge—that is, try to see them as faces, as we asked them after every trial

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how many faces they perceived. Thus, it seems critical that items are processed in depth during encoding in order to achieve the benefits promoted by meaningfulness.

Whether—and to what extent—the increases in capacity we observe happen during encoding and persist across the delay, or occur only from reduced noise accumulation during storage, is an interesting question for future research. We believe that either interpretation is very much in line with our main conclusion—namely, that working memory capacity is not fixed but adaptable to the type of stimuli being remembered. Indeed, it is plausible that these two possibilities are fundamentally the same, if, as many propose, visual working memory is really "sustained perception," with attention-like mechanisms continuing to keep the perceptual activity going over a delay (e.g., Chun, 2011). Under such an account, the improved persistence of perceived faces over the delay is exactly the same thing as improved encoding of them into working memory, and improved encoding is likely necessary to allow the greater maintenance activity we observe. Consistent with this, an exploratory analysis of Experiment 3 suggests that the CDA benefits here arise even while the stimuli are on the screen: Excluding the initial perceptual processing window (300 msec), we find a reliable amplitude difference between one versus three objective faces during the time the stimuli are on the screen, $t(18) = 2.96$, $p = .0084$. This is consistent with other work finding CDA-like e_k; activity is present even while stimuli are on the screen, if they must be held actively in mind during this time (Tsubomi, Fukuda, Watanabe, & Vogel, 2013; Drew, Horowitz, Wolfe, & Vogel, 2012; Emrich, Al-Aidroos, Pratt, & Ferber, 2009).

Many studies have shown that existing knowledge or familiarity with a stimulus improves the ability to maintain information not only in long-term memory but also over short delays, often termed *long-term working memory* (Ericsson & Kintsch, 1995). However, it has been unclear the extent to which such benefits arise from changes in active storage in working memory per se, or from the usage of "long-term" memory systems or other forms of more passive storage that can be utilized in the short-term maintenance of information. Both neurally and cognitively, the active component of working memory (sometimes referred to as the "focus of attention") is particularly important as it seems to be the element of working memory most responsible for capacity limits and correlations with broader cognitive abilities (e.g., Cowan, 2005). By contrast, other forms of memory sometimes called working memory but which are nonactive—like activated long-term memories or long-term working memory—are widely acknowledged to be influenced by knowledge and meaningfulness (Ericsson & Kintsch, 1995), but are often considered not to be core elements of working memory capacity (Feldmann-Wüstefeld, Vogel, & Awh, 2018). We here show that this active component of working memory (as indexed by the CDA) is strongly affected by the meaningfulness of the stimulus being remembered. If a stimulus connects to a concept and is thus perceived as meaningful, the active storage component of memory capacity is greater.

Whereas a large body of work has shown benefits for objects of expertise in short-term storage (e.g., Curby et al., 2009), one line of recent work has claimed that expertise effects in visual working memory may sometimes arise from enhanced consolidation of items into memory rather than increased capacity per se (Xie & Zhang, 2017b, 2018), although capacity increases have also been found (Xie & Zhang, 2017a). Importantly, in the current work with our within-subject, perceptual manipulation of meaningful recognition and concurrent electrophysiological recordings, we show that active storage in working memory itself is impacted by meaning, with no change over the time course of the CDA component as suggested by a consolidation-based account. We also use an encoding time that is long enough to avoid encoding limits (1000 msec), even according to the work arguing for consolidation limits (e.g., Xie & Zhang, 2018). The kind of meaningfulness Xie and Zhang manipulate is quite different than in the current work, as unlike the perception of a stimulus as a face-enhanced memory in their experiments likely requires retrieval of specific information from long-term memory.

How might conceptual knowledge or other crystallized long-term memories enhance active storage in working memory? One possibility is that once a stimulus is perceived as meaningful (e.g., as a face), more useful information is being extracted and stored relative to when a stimulus is perceived as meaningless. In that case, the ability to maintain this information in working memory flexibly adjusts depending on the stimulus input—possibly allowing a broader set of features to be remembered and actively maintained for holistic objects relative to arbitrary shapes. This would also limit interference between the neural populations that must be held active (e.g., Cohen, Konkle, Rhee, Nakayama, & Alvarez, 2014). Because having more crystallized knowledge about an object or object category results in more relevant neural populations being activated, attentional mechanisms can maintain more active information successfully when dealing with meaningful objects (Wyble et al., 2016). Thus, knowledge may serve as a "hook" that helps recruit the critical neural populations that are both more relevant and more distinct, thereby facilitating active maintenance of meaningful information.

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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