Bistable perception of symbolic numbers

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Numerals, that is, semantic expressions of numbers, enable us to have an exact representation of the amount of things. Visual processing of numerals plays an indispensable role in the recognition and interpretation of numbers. Here, we investigate how visual information from numerals is processed to achieve semantic understanding. We first found that partial occlusion of some digital numerals introduces bistable interpretations. Next, by using the visual adaptation method, we investigated the origin of this bistability in human participants. We showed that adaptation to digital and normal Arabic numerals, as well as homologous shapes, but not Chinese numerals, biases the interpretation of a partially occluded digital numeral. We suggest that this bistable interpretation is driven by intermediate shape processing stages of vision, that is, by features more complex than local visual orientations, but more basic than the abstract concepts of numerals.

Introduction

The sense of number endows animals with a better chance of survival by bringing behavioral advantages to daily activities like foraging and avoiding predation (Nieder, 2020). Psychophysical and neuroscientific studies using arrays of dots demonstrated that the

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neural mechanisms for processing non-symbolic number information are shared among humans and other animals (Burr & Ross, 2008; Burr, Anobile, & Arrighi, 2017; Harvey, Klein, Petridou, & Dumoulin, 2013; Hubner & Schutz, 2017; Nieder, 2012; Nieder, 2013; Nieder, 2016; Park, DeWind, Woldorff, & Brannon, 2016; Tsouli et al., 2022; Viswanathan & Nieder, 2013).

However, one aspect that dissociates humans from other animals is the ability to recognize symbolic numbers. The semantic understanding of those characters representing numbers, that is, numerals, enables humans to have a much more exact and flexible appreciation of the numerical world (Wiese, 2003), and also mathematical and logical skills that lead to significant developments in sciences, technologies, and social economics.

In the human brain, patches on the inferior temporal gyrus represent symbolic numbers, such as Arabic numerals (Cai, Hofstetter, & Dumoulin, 2023; Conrad, Pollack, Yeo, & Price, 2023; Shum, Hermes, Foster, Dastjerdi, & Rangarajan, 2013; Yeo, Pollack, Merkley, Ansari, & Price, 2020; Yeo, Wilkey, & Price, 2017). However, as of yet, we do not know how the recognition of symbolic numbers is generated through visual processing from local orientation to complex shapes, category information, and semantic recognition (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Riesenhuber & Poggio, 1999).

Bistable perception is a powerful tool for investigating the relationship between perception and visual processing (Blake & Logothetis, 2002; Brascamp & Shevell, 2021; Leopold & Logothetis, 1999; Rodriguez-Martinez & Castillo-Parra; 2018; Schneider, Kemper, Emmerling, De Martino, & Goebel, 2019; Sterzer, Kleinschmidt, & Rees, 2009). Specifically, it enables scientists to examine what factors lead to a specific interpretation while the physical input to the visual system remains identical.

Here, we introduce a bistable perception of symbolic numbers by partial occlusion. We used digital numerals that widely exist in modern society. Because of their simple design, they are applied to various consumer electronics, such as calculators and traffic countdown timers (Figure 1A). The semantic interpretation of digital numerals can be manipulated easily by adding or removing one stick from the character, such as those shown in Figure 1B, where the interpretation is altered between 5 and 9, and 6 and 8. Inspired by this feature, we found that a partial occlusion of these symbolic characters results in bistable semantic interpretations. Such as the case in Figure 1C, people recognize this occluded digital numeral as either 6 or 8. This phenomenon can also be extended to a group of sequentially arranged numerical characters, because the partial occlusion of them leads to multiple interpretations that occur most noticeably in monotonically increasing and decreasing orders (Figure 1D). This bistable interpretation of digital numerals is also present in our daily life. Supplementary Video S1 demonstrates an example of a traffic countdown timer in the city. When part of the numerical character is occluded by the protective cover, starting from one moment, people tend to see the numbers being counted from 5 to 9 instead of being counted from 9 to 5.

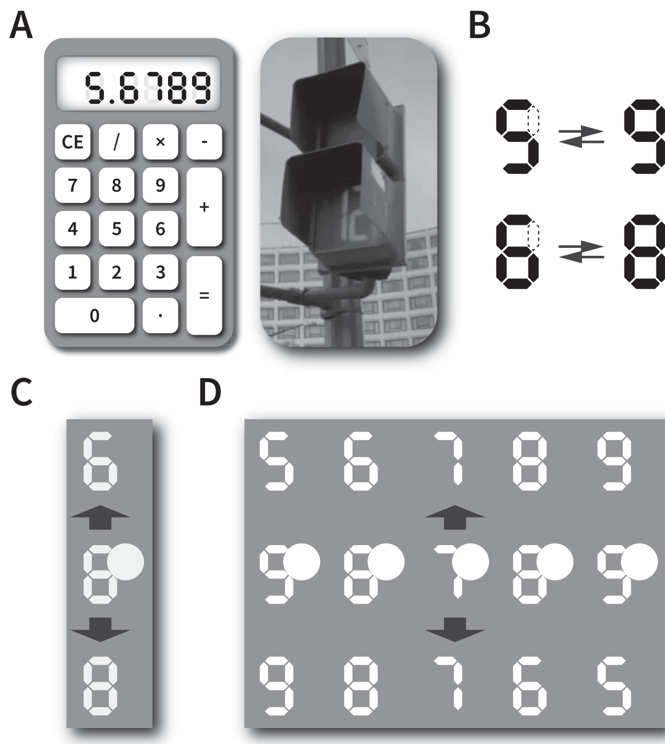

Figure 1. Digital numerals and perceptual bistability. (**A**) Digital numerals are shown in the display of a calculator (left) and traffic countdown timer (right). (**B**) Adding or removing the top-right stick of some digital numerals changes their semantic interpretations. (**C**) The middle digital numeral is partially masked by a disk of the same luminance and therefore can be interpreted as either 6 (top character) or 8 (bottom character). (**D**) The manipulation of occlusion that is applied to a group of numerical characters (middle row) causes two different interpretations of ordered sequences, e.g., they can be interpreted as an ascending (top row) or descending (bottom row) order.

In this study, we aimed to shed light on the mechanisms underlying the visual processing of symbolic numbers by psychophysically measuring and manipulating the bistable perception of occluded digital numerals.

Adaptation is an effective psychophysical method to selectively manipulate the sensitivity of the visual system and target the cortical loci that contribute to visual functions (Frisby, 1979; Kohn, 2007; Webster,

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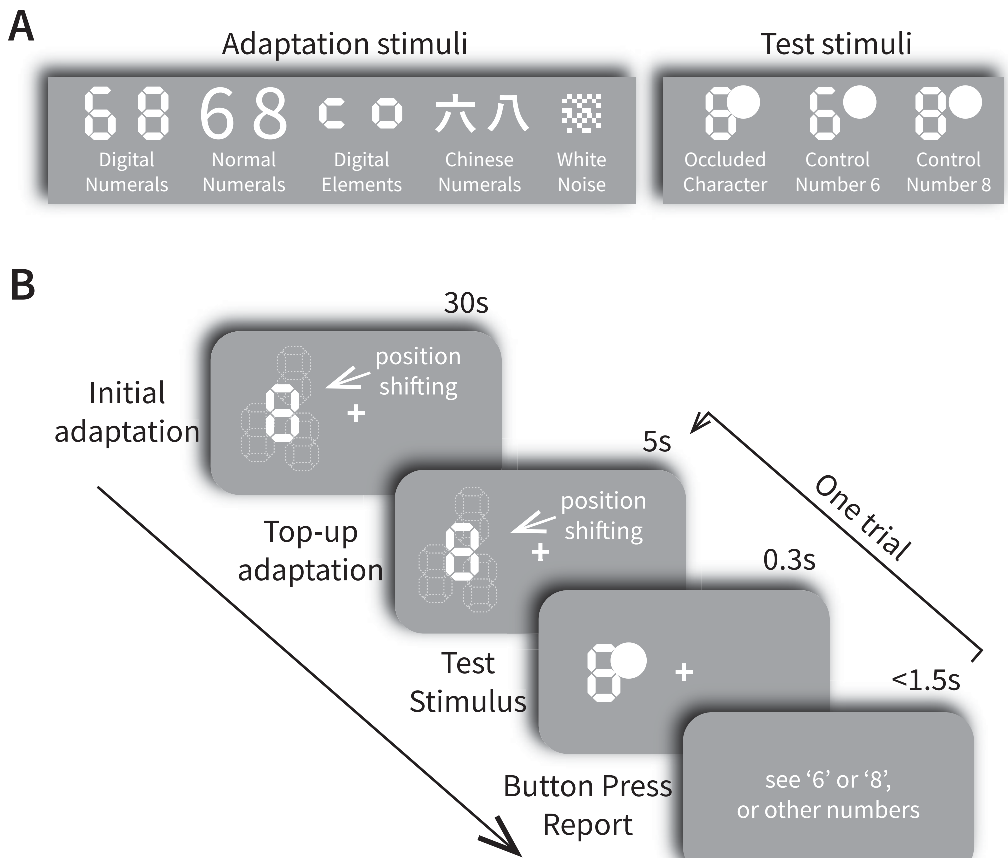

Figure 2. Illustrations of stimuli designs and task time series. (**A**) Five types of visual stimuli were used as adaptation stimuli, including two kinds of numerical characters (digital and normal Arabic numerals), one kind of shape stimulus (digital elements), one kind of Chinese numerals (semantically representing 6 and 8), and control stimulus (white noise). Three characters were presented as test stimuli after adaptation, including one occluded character (with a mask covering the top right part), and two control characters (with a mask on the top right side, but no coverage). (**B**) Each experimental block started with an initial adaptation period where normal numerical characters or shapes were presented for 30 seconds. It was followed by a loop of trials. Each trial sequentially contains a top-up (5 seconds) adaptation to the same adaptation stimuli as used in the initial adaptation, a presentation period for the test stimulus, and a report time window, participants were asked to report whether they recognize the occluded numeral as 6 or 8, or other numbers, by pressing one of three buttons on a gaming pad.

2015). For example, if there were clusters of neurons selectively encoding a given numeral (such as 6), prolonged exposure to the visual presentation of that numeral will decrease the responsiveness of those neurons and potentially influence the perceptual recognition of that number. Therefore, testing how adaptation impacts the perception of partially occluded digital numerals should reveal the perceptual and neural mechanisms underlying the visual processing of numerals.

In this study, we used a psychophysical task using several representative symbols and shapes as adaptation stimuli, that is, digital and normal Arabic numerals, digital elements, and Chinese numerals (Figure 2A, left). We hypothesize that the different adaptation stimuli affect different visual processing stages. Therefore, we evaluated the contributions of processing each stage to the perceptual bistability by assessing whether the semantic recognition of occluded digital numerals could be biased under each adaptation condition (Figure 2A, right). We found that adaptation to stimuli that shared certain shape similarities with the partially occluded digital numerals resulted in a strong perceptual bias. In contrast, other adaptation stimuli with the same semantic meaning but different shapes (Chinese numerals) did not have such an effect. Results indicate that the perceptual bistability of digital numerals has a neural origin, which is involved in processing complex visual form information.

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Methods

Participants

Seventeen adults (9 females and 8 males; ages ranging from 19 to 31 years) with normal or corrected-to-normal visual acuity participated in the experiment. Tasks were performed after the participants signed a written informed consent that included explanations of voluntary participation, experimental safety, and freedom to withdraw, as well as an agreement on the data sharing policy. All participants were born in Japan and were proficient in Japanese and in reading Chinese characters. All participants passed the battery of tests assessing visual functions, including acuity, astigmatism, and binocular stereopsis before the main experiment. The study protocol was approved by the Ethics Committee of National Institutes of Natural Sciences (protocol number: EC01-64). We note that the data from one participant were excluded from analyses owing to excessive eye movements (as discussed elsewhere in this article). Therefore, we report the data acquired from 16 participants (8 females and 8 males; ages ranging from 19 to 31 years).

Apparatus

Visual stimuli were presented on a BenQ 24.5-inch display (ZOWIE XL2546K, BenQ, Taipei) with a spatial resolution of 1,920 × 1,080 pixels and a refresh rate of 240 Hz. The luminance of the display was linearly scaled using gamma calibration. A self-designed chinrest mounted 65 cm away from the display was used to stabilize participants' heads and to keep the observation distance constant. Fixation was monitored by an eye tracking system (LiveTrack Lightning, Cambridge Research Systems, Rochester, UK); the camera was placed in front of the chinrest and 18 cm away from the eyes and tracked the positions of both eyes online. Visual stimuli generation and online data analysis were performed using a workstation (Dell Precision 3650, Dell, Round Rock, TX) operated under the Linux system (Ubuntu 20.04 LTX). Participants used a gaming pad (Retro-Bit Legacy 16, Retro-Bit, Pomona, CA) to report their perceptions.

Stimuli

Visual stimuli were designed using MATLAB Psychtoolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007 http://psychtoolbox.org/; Pelli, 1997). All stimuli were drawn in white and presented against a medium-gray background. During stimulus presentation, a white fixation cross of 0.5° in diameter was also presented at the center of the display (Figure 2B).

We used five different types of adaptation stimuli (Figure 2A, left): 1) digital numerals 6 and 8, 2) normal Arabic numerals 6 and 8, 3) two digital elements representing the upper part of digital numerals 6 and 8, 4) Chinese numerals 6 and 8 (六 and 八 corresponding with 6 and 8), and 5) white noise patterns as control stimuli. There were two white noise stimuli, generated by random shuffling of the pixels in the two digital numerals. Because we did not find any significant difference in behavioral responses between the two white noise stimuli, we present the averaged results of the two white noise stimuli in the population analysis. The height of the adaptation stimuli was 200 pixels (corresponding with a visual angle of approximately 5°, the height was halved in the digital element stimuli). The width of the digital and normal Arabic numerals, the digital elements, and the white noise pattern were 124 pixels (3.3°), and the width of the Chinese numerals was 216 pixels (5.8°) because of their specific design.

We used three test stimuli (Figure 2A, right). The first one was a digital numeral with a white circular mask placed over the right upper part. The second and third ones were control test stimuli. Each control test stimulus was composed of either the digital numeral 6 or 8 with the same mask but without overlap so that the digital numerals could be easily recognized as either 6 or 8 without ambiguity. The test digital numerals were of the same size as the adaptation digital numerals, whereas the diameter of the mask was 178 pixels (4.8°). The control test stimuli were used to make sure that participants were always making valid responses during the task. Because all participants responded correctly to the control test stimuli in 100% of the trials, we considered their perceptual responses to the partially occluded stimuli also reliable.

Figure 2B depicts the time series of the experiment. Both adaptation and test stimuli were presented in either the left or right visual field. The adaptation stimuli were presented horizontally and on average 6° away from the fixation cross, while their positions were randomly shifted every second within a circular area of 6°. Such position shift was used to prevent low-level adaptation effects in early visual areas (e.g., the primary visual cortex) where the neurons have smaller receptive field sizes, and also give enough distance from the fixation point to ensure that they did not fall onto the fovea. The test stimuli were presented at an eccentricity of 6°, but were kept static during presentation.

Both the adaptation and test stimuli were shown on either the left or right side of the visual field within one task block, but their positions were changed to the other side in the next task block.

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Procedure

During the experiment, participants were asked to maintain fixation at the central white cross, while paying attention to the peripheral visual stimuli. The initial adaptation period lasted for 30 seconds before the loop of trials (see Supplementary Videos S2–S4). In each trial, a 5-second top-up adaptation to the same stimulus was followed by a 300-ms presentation of the test stimulus. At the end of each trial, participants were instructed to report whether they recognize the test stimulus as 6 or 8, or other numbers, by pressing the *L* or *R* or *A* button on the gaming pad (Figure 2B). The experiment was divided into five sessions based on five different adaptation stimuli as shown in Figure 2A left. There were four blocks in each session; in two blocks, the adaptation stimulus was number 6 or the element corresponding with the number 6, and in the other two blocks, the number 8 or the element corresponding with the number 8. In both pairs of blocks, stimuli were presented on either the left or right visual field in one block and the opposite visual field in the other block. Within each block, every combination of the adaptation stimulus and the three test stimuli (Figure 2A, right) was repeated 10 times (adaptation to white noise was repeated 5 times). Thus, there were a total of 20 repetitions for each combination (10 repetitions for white noise and test stimuli combination). As a result, there were 540 trials in the whole experiment. Each block consisting of 30 trials lasted approximately 5 minutes (15 trials and 2.5 minutes for the white noise adaptation condition), resulting in a 90-minute experiment.

Data analysis and quantification

The proportions of trials in which participants recognized the occluded digital numeral as either 6, 8, or other numbers were calculated for each adaptation condition. We quantified a perceptual bias in each condition by calculating the bias index using the following equation:

$$Bias\ index = \frac{N_6 - N_8}{N_6 + N_8}, \quad (1)$$

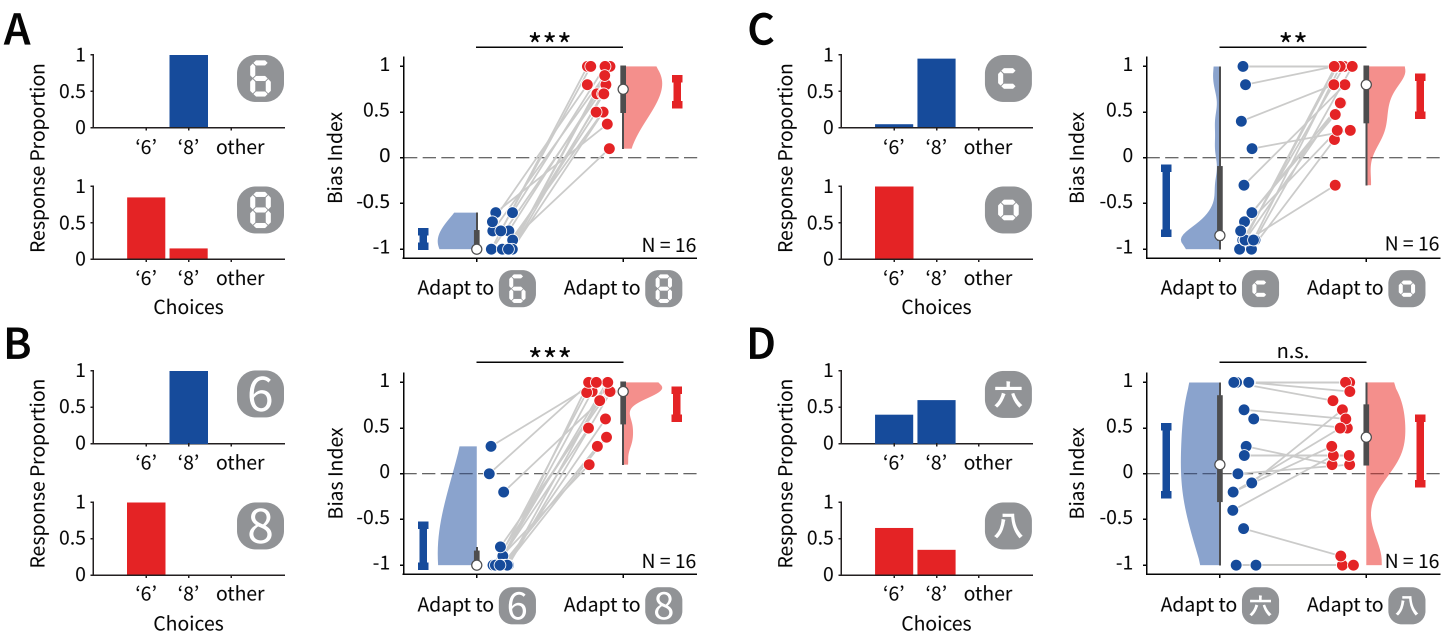

Figure 3. Single participant and populational results of four adaptation conditions. (**A**) (Left) Response proportions of one participant (P1) reporting seeing 6, 8, or other numbers, after adaptation to digital numeral 6 (top) and digital numeral 8 (bottom). The results show strong but opposite perceptual biases in two adaptation conditions. (Right) Populational results of the same adaptation conditions from 16 participants. Similar to the results of a single participant, bias indices of two conditions distribute oppositely and are significantly different from each other (blue, adaptation to digital numeral 6; red, adaptation to digital numeral 8). Dots depict the data from individual participants. Dots of different conditions but the same participant are connected by gray lines. Shadows represent a kernel density estimate of the data. The error bar depicts a 95% confidence interval. (**B**) Same description as in (**A**), but the conditions are adaptation to normal Arabic numerals 6 and 8. (**C**) Same description as in (**A**), but the conditions are adaptation to digital element ⊏ and ☐. (**D**) Same description as in (**A**), but the conditions are adaptation to Chinese numerals 六 and 八. There is no significant difference between two conditions. ***$p < 0.001$; **$p < 0.01$; n.s.: not significant in Kruskal–Wallis one-way analysis of variance.

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where N_6 and N_8 indicate the number of trials in which participants reported "6" and "8," respectively. The bias index ranged from −1 to 1; positive values indicate that participants reported recognizing the occluded numeral as 6 more often than 8 and negative values indicate that participants reported 8 more often than 6. The population distributions of the bias index across 16 participants are illustrated using a violin plot (https://zenodo.org/records/4559847) in Figure 3, where the shadow represents a kernel density estimate of the data. The statistical significance of the difference in bias indices between adaptation conditions was tested by Kruskal–Wallis one-way analysis of variance. We also calculated Cohen's d to measure the effect size. To further evaluate the weight of perceptual bias differences between adaptation to numbers 6 and 8, we performed the Bayesian Wilcoxon signed-rank test and calculated Bayes factors (BF_{10}) for each adaptation condition using the JASP statistical software (https://jasp-stats.org/). A larger BF_{10} indicates stronger evidence for different perceptual biases between adaptation to numbers 6 and 8 whereas while a smaller BF_{10} indicates evidence for the same perceptual biases.

The eye fixation stability of each participant was monitored to determine whether their data were included in the statistical analysis. Data from one participant were excluded from the analysis owing to an excessive amount of saccadic eye movement to the adaptation stimuli.

Code availability

Data and code for visual stimuli presentation as well as data analysis are available in a public repository (https://osf.io/2np7e/).

Results

We first tested whether adaptation to the digital numerals 6 and 8 (Figure 2A, left), which share the same shape as the test stimuli (Figure 2B, right), biases the recognition of the partially occluded digital numeral. Results from one representative participant (P1) are illustrated in Figure 3A (left). After adaptation to digital numerals, the responses to the partially occluded digital numeral showed clear perceptual biases despite the ambiguity caused by the partial occlusion. Specifically, after adaptation to the digital numeral 6, the participant always reported the test stimulus as the number 8 (Figure 3A, top left; response proportions: 0% for 6; 100% for 8, and 0% for other numbers), whereas after adaptation to digital numeral 8, the participant reported the test stimulus as number 6 in most trials (Figure 3A, bottom left; response proportions: 85% for 6, 15% for 8, and 0% for other numbers).

This perceptual bias was confirmed at the population level (Figure 3A, right). The bias indices of all 16 participants were negative under the adaptation condition of digital numeral 6 (*mean* = −0.89; 95% confidence interval [CI]: ± 0.08), indicating that participants tended to see the test stimulus as 8. In contrast, the bias indices were all positive under the adaptation condition of the digital numeral 8 (*mean* = 0.72 ± 0.14 [95% CI]), indicating that participants tended to recognize the test stimulus as 6. The perceptual biases were significantly different between the two adaptation conditions ($d = 7.00$; $p = 3.45 \times 10^{-6}$; $BF_{10} = 1.1 \times 10^4$). These results show that the recognition of partially occluded digital numerals was biased strongly by visual adaptation. This effect of adaptation suggests that the bistable perception is not driven by the subjective interpretation of the semantics of numerals, but constitutes a visual information processing mechanism.

Next, we asked which level of visual processing determines the bistable perception of the occluded digital numeral. We note that the position shifting of adaptation stimuli in our task paradigm already suggests that the perceptual biases do not happen in the early stages of visual processing (such as the primary visual cortex), where the receptive fields of neurons are relatively small and the adaptation effect is strictly localized (Kohn, 2007; Kohn & Movshon, 2003).

To investigate whether the later stages of visual processing play a role in bistable perception, we introduced normal Arabic numerals as adaptation stimuli (Figure 2A, left). Normal Arabic numerals and digital numerals have similar global appearances, but differ in their local visual features; digital numerals are composed of horizontally and vertically oriented intermittent straight sticks, whereas normal Arabic numerals are composed of continuous curvatures. Because primary visual processing stages are sensitive to local feature differences and later stages are not (Kravitz et al., 2013), examining whether adaptation to the normal Arabic numerals influences the recognition of the occluded digital numeral allowed us to answer whether later stages of visual processing played a fundamental role in the perceptual bistability of digital numerals. For example, compared with early visual areas, intermediate visual areas such as V4, are driven less by local features of the stimulus (e.g., edges) but rather by more complex features (e.g., curvature) (Dumoulin & Hess, 2007; Gallant, Braun, & Van Essen; 1993; Pasupathy & Connor, 2002; Wilkinson et al., 2000; Wilson, Wilkinson, & Asaad, 1997).

Results showed that adaptation to normal Arabic numerals is comparable with adaptation to digital numerals, both at the single participant level (Figure 3B, left; response proportions of adaptation to normal

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Arabic numeral 6: 0% for 6, 100% for 8, and 0% for other numbers; response proportions of adaptation to normal Arabic numeral 8: 100% for 6, 0% for 8, and 0% for other numbers) and at the population level (Figure 3B, right; bias indices of adaptation to normal Arabic numeral 6, *mean* = −0.79 ± 0.22 [95% CI]; bias indices of adaptation to normal Arabic numeral 8, *mean* = 0.76 ± 0.15 [95% CI]; $d = 4.07$, $p = 9.77 \times 10^{-7}$; $BF_{10} = 2.8 \times 10^3$). The adaptation effects of normal Arabic numerals further support the idea that bistable recognition of the occluded digital numerals is established later in the visual processing stream, rather than in the early stages.

Last, we investigated whether the processing of semantics plays a critical role in generating the bistable perception. We first tested the effect of adaptation to digital elements (the upper parts of the digital numerals) (Figure 2A, left); this modification removed the semantic components of the digital numerals while preserving some shape similarities. The results were similar to those in digital and normal Arabic numerals adaptation conditions at both the single participant level (Figure 3C, left; response proportions of adaptation to digital element ⊏, 5% for 6, 95% for 8, and 0% for other numbers; response proportions of adaptation to digital element □, 100% for 6, 0% for 8, and 0% for other numbers) and population level (Figure 3C, right; bias indices of adaptation to digital element ⊏, *mean* = −0.47 ± 0.36 [95% CI]; bias indices of adaptation to digital element □, *mean* = 0.67 ± 0.21 [95% CI]; $d = 1.98$, $p = 0.0065$; $BF_{10} = 1.1 \times 10^3$), although the effect size of differences between two adaptation conditions was lower than that obtained under the adaptation conditions of digital and normal Arabic numerals.

As opposed to digital elements, Chinese numerals share the same meanings as digital numerals, although their shapes are different (Figure 2A, left). We predicted that, if the semantic processing stage plays a role in bistable perception, there would be perceptual bias after adapting to Chinese numerals. To ensure a valid adaptation, all participants were born in Japan and fluent in both Chinese and Arabic numerals. Results showed that adaptation to Chinese numerals did not bias perceptual interpretation of the occluded digital numerals at either the single participant level (Figure 3D, left; response proportions of adaptation to 六, 40% for 6, 60% for 8, and 0% for other numbers; response proportions of adaptation to 八, 65% for 6, 35% for 8, and 0% for other numbers) or the population level (Figure 3D, right; bias indices of adaptation to Chinese numeral 六, *mean* = 0.14 ± 0.37 [95% CI]; bias indices of adaptation to Chinese numeral 八, *mean* = 0.25 ± 0.36 [95% CI]; $d = 0.15$, $p = 1.00$, $BF_{10} = 0.31$). Moreover, the bias indices of adaptation to Chinese numerals are comparable with that in the control condition (adaptation to white noise) at both the single participant level (Supplementary Figure S1, left; response proportions of adaptation to white noise: 50% for 6, 50% for 8, and 0% for other numbers) and the population level (Supplementary Figure S1, right; bias indices of adaptation to white noise, *mean* = 0.22 ± 0.38 [95% CI]).

These results suggest that semantic processing mechanisms do not take a major role in the perceptual bistability of the partially occluded digital numeral.

Discussion

In this study, we demonstrate that partial occlusion of digital numerals can induce bistability in their semantic interpretation. Adaptation to visual stimuli that share shape similarities with occluded digital numerals reduces perceptual ambiguities and leads to unique semantic recognition. Our results indicate that the bistable perception of the occluded digital numerals relies neither on early stage visual processing nor semantic recognition mechanisms (Figure 4). Rather, it largely depends on the mid-level visual processing stages, which encode complex shapes and symbolic number forms (Conrad et al., 2023; Shum et al., 2013; Yeo et al., 2020; Yeo et al., 2017) in a manner invariant

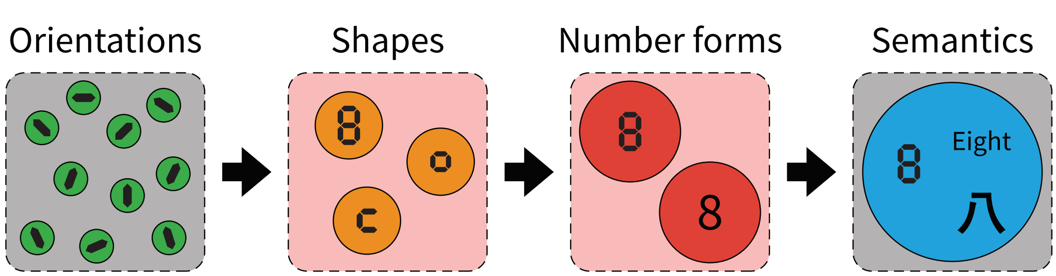

Figure 4. Illustration of the hierarchical visual information processing that endows us with capabilities ranging from the perception of simple orientations to the sensation of complex shapes and number forms, and finally to the semantic understanding of symbols, words, and characters. Our results from visual adaptation implicate the function of middle stages (marked by red squares) in the perceptual bistability of occluded digital numbers.

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to stimulus positions (Ito, Tamura, Fujita, & Tanaka, 1995; Logothetis & Sheinberg, 1996; Vogels & Orban, 1996).

Occlusion generates perceptual bistability

Do the occluded digital numerals elicit bistable perception? On the one hand, we refer to the resulting percept as bistable perception because the occluded digital numerals have two dominant perceptual interpretations. Furthermore, adaptation can bias the perceptual interpretation one way or the other. In contrast, in traditional bistable stimuli, such as the Necker cube or Rubin's vase, perception alternates spontaneously between these two interpretations over time, and for many vision researchers, bistable perception implies spontaneous perceptual alternations. Subjectively, some observers do report perceptual alternations, whereas others do not when they observe the occluded digital numerals for a long duration. Regardless, the perceptual alternations of the occluded digital numerals are not as inevitable or salient as traditional phenomena of bistable perception. From this perspective, the occluded digital numerals may be considered a special case of visual ambiguity. However, implicit ambiguity in neural representations is pervasive, and resolving ambiguity is a fundamental and ubiquitous process (Brascamp & Shevell, 2021). The occluded digital numerals are a special case of visual ambiguity with two stable percepts and likely results from competition between neural representations; therefore, we feel the term bistable perception is more appropriate than generalized visual ambiguity.

In a natural environment, humans often encounter situations where objects of interest are partially covered (Figure 1A, right). Nevertheless, recognition of those partially occluded objects takes little effort for the visual system, despite the incomplete information. This phenomenon of visual completion has been studied intensively in psychophysics (Nakayama, Shimojo, & Silverman, 1989; Shimojo & Nakayama, 1990; Tse, 1999), physiology (Albright & Stoner, 2002), and neuroimaging (Ban et al., 2013; Thielen, Bosch, van Leeuwen, van Gerven, & van Lier, 2019). Usually, partial occlusion results in perceptual filling in of the visual information made unavailable by the occluder, and the literature has mainly focused on studying the visual completion of occluded objects (Sekuler & Palmer, 1992). However, not all cases of occlusion induce visual filling in; in some cases, the covered area may be interpreted as containing no relevant information.

Our partially occluded digital numerals can be considered one of such cases because both interpretations are equally probable and the digital numerals are meaningful, whether or not the occluded part is filled in. For example, in our experiment, the partially occluded numerals (Figure 2A, right) may be interpreted as either the number 6 or 8, depending on whether the area behind the white disk is filled in with a vertical stick. One possible reason for this specific phenomenon is that numerals, such as 6 and 8, are well-learned symbolic characters, and robust visual shape templates exist inside human brains. When occurrences of two numerals (e.g., 6 and 8) are equally probable, the perceptual system must resolve competition between these two perceptual interpretations as occluded digital numerals are processed based on perceptual templates, and such competition causes bistable perception.

We note that there was a considerably large individual difference in the control condition (adaptation to white noise; see Supplementary Figure S1, right). Specifically, some participants consistently reported that they perceived the occluded digital numeral as 6, or consistently as 8, whereas all participants showed the same trend of perceptual bias after adaptation to digital numerals (Figure 3). The reason why this large individual difference was observed in the control condition is an open question.

Visual adaptation breaks down the bistable state of partially occluded numerals

In our experiment, the adaptation to numerals and shapes of similar appearances broke down the bistable state and led to a unique perceptual interpretation of the partially occluded digital numerical character. One possible explanation is that adaptation suppresses the sensitivity of the neural mechanism that encodes a certain numerical form. To be specific, the response state of mechanisms encoding numerals 6 and 8 are normally balanced with each other, contributing similarly to the interpretation of a partially occluded numeral and therefore producing perceptual bistability. However, adaptation to the digital numeral 6 led to decreased sensitivity of the corresponding encoding mechanism, resulting in a higher response state of the neural mechanism that encodes digital numeral 8. This process produces a perceptual bias of the partially occluded digital numeral toward the number 8, and vice versa.

The role of semantic mechanism on bistable perception of digital numerals

Adaptation to Chinese numerals did not induce significant perceptual biases between 6 and 8. It is reasonable to explain this result solely based on the perceptual mechanisms in the early and middle visual

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processing stages because Chinese numerals do not share both local and global shape similarities with digital numerals. Meanwhile, because all participants are familiar with Chinese numerals that share semantic information with digital numerals, a lack of evidence on the adaptation effect by Chinese numerals may suggest that the semantic mechanism is not necessary for adaptation effects on the perceptual bistability of partially occluded digital numerals. This idea is further supported by results showing statistically significant perceptual biases induced by adaptation to semantically meaningless digital elements.

Nevertheless, we note that we cannot fully rule out the possibility that the contribution of semantic mechanisms to perceptual bistability can be observed if we use an experimental approach causing different effects on perception, such as priming, as we discuss in the next paragraph.

Visual adaptation and perceptual priming

Semantic recognition of symbolic numerals is not only based on visual processing but also on cognitive information processing of numerosity and memory. Our study aims to investigate the former aspect, by using visual adaptation paradigms in which prolonged exposure to visual stimuli reduces the sensitivity to stimuli of the same category (Webster, 2015). In contrast, a series of experimental psychology and cognitive neuroscience works demonstrated that perceptual priming paradigms activate the knowledge or associated memory that affects the perceptual interpretation of ambiguous stimuli (Schacter & Buckner, 1998; Tulving & Schacter, 1990). According to the literature, the major difference between visual adaptation and perceptual priming is the resulting perceptual effects (Webster, 2015; Wiggs & Martin, 1998), that is, visual adaptation often causes perceptual interpretation opposite to the adaptation stimuli (Anstis, Verstraten, & Mather, 1998), although perceptual priming often leads to an interpretation toward the priming stimuli. For instance, in the recognition of an ambiguous object after the prior experience of an unambiguous object, participants identified the ambiguous object as having a similar shape as the priming object (Chang, Baria, Flounders, & He, 2016; González-García, Flounders, Chang, Baria, & He, 2018; Hsieh, Vul, & Kanwisher, 2010; Perez, Cook, & Peterson, 2020; Squire, Frascino, Rivera, Heyworth, & He, 2021; van Loon, Fahrenfort, van der Velde, Lirk, & Vulink, 2016). In contrast, the results of our experiment are consistent with findings in adaptation studies, because visual adaptation to the numeral 8 breaks down the ambiguous occluded digital numeral and induces perception biases to 6, and vice versa. It is possible that the perceptual priming of numerals 6 or 8 also affects perceptual interpretation of occluded digital numerals but we speculate that priming causes different perceptual effects.

Conclusions

Our findings lead us to conclude that the perceptual bistability of partially occluded digital numerals originates mainly from competitions in visual processing stages involved with processing global shapes and number forms. Neither early visual or semantic processing is likely to be involved in the interpretation of bistable digital numerals.

Keywords: number, numeral, bistable perception, adaptation, occlusion

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Supplementary material

Supplementary Video S1. The traffic countdown timer is partially covered by the protective roof. Although the digital numerals (from 9 to 5) are temporally aligned in a descending order, they can also be perceptually interpreted as aligned in an ascending order from 5 to 9.

Supplementary Video S2. A demo video showing the effect of visual adaptation. Digital numerals of 6 and 8 are presented on the left and right visual fields, respectively. Two occluded digital numerical characters of the same shape are shown on both visual fields after adaptation. Although the test stimuli don't have any difference, the occluded character on the left visual field looks more like 8, and the other one on the right side looks more like 6.

Supplementary Video S3. A demo video showing the stimuli presentation. The adaptation stimulus of the digital numeral 6 on the right visual field is presented for 30 seconds, after that the occluded test stimulus is shown for 0.3 seconds.

Supplementary Video S4. A demo video showing the stimuli presentation. The adaptation stimulus of the digital numeral 8 on the right visual field is presented for 30 seconds, after that the occluded test stimulus is shown for 0.3 seconds.

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