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A subcortical magnocellular pathway is responsible for the fast processing of topological properties of objects: A transcranial magnetic stimulation study

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Abstract

Rapid object recognition has survival significance. The extraction of topological properties (TP) is proposed as the starting point of object perception. Behavioral evidence shows that TP processing takes precedence over other geometric properties and can accelerate object recognition. However, the mechanism of the fast TP processing remains unclear. The magnocellular (M) pathway is well known as a fast route to convey "coarse" information, compared with the slow parvocellular (P) pathway. Here, we hypothesize that the fast processing of TP occurs in a subcortical M pathway. We applied single-pulse transcranial magnetic stimulation (TMS) over the primary visual cortex to temporarily disrupt cortical processing. Besides, stimuli were designed to preferentially engage M or P pathways (M- or P-biased conditions). We found that, when TMS disrupted cortical function at the early stages of stimulus processing, non-TP shape discrimination was strongly impaired in both M- and P-biased conditions, whereas TP discrimination was not affected in the M-biased condition, suggesting that early M processing of TP is independent of the visual cortex, but probably occurs in a subcortical M pathway. Using an unconscious priming paradigm, we further found that early M processing of TP can accelerate object recognition by speeding up the processing of other properties, e.g., orientation. Our findings suggest that the human visual system achieves efficient object recognition by rapidly processing TP in the subcortical M pathway.

KEYWORDS

early processing, magnocellular pathway, object recognition, subcortical pathway, topological perception, transcranial magnetic stimulation

1 | INTRODUCTION

The human visual system is characterized by rapid detection of objects in the environment and relatively slow processing of the detailed features of objects. Fast detection of objects is important for our survival, such as to avoid potential dangers. Imagine an object running past you in the forest, and you will quickly mount a defensive response before you can recognize the object. How the visual system constructs object perception in early stages is a fundamental question in vision research. A theory of topological perception has been proposed to address this question, which holds that the extraction of topological property (TP) is the starting point of object perception (Chen, 1982, 2005). Topology, a branch of mathematics, describes the invariant characteristics of shapes across continuous smooth transformations, including twisting, stretching, bending but not tearing. The number of holes (hereafter referred to as hole) remains constant in this kind of rubber-sheet distortion and hence is a TP (Chen, 1982, 2005). For instance, a donut (one hole) is topologically different from a pizza (no holes). In addition to holes, connectivity and closure are also TP, which have also been proposed by other researchers as basic units of visual form perception, for example, in the texton theory proposed by Julesz (1981). The topological perception theory has been supported by sufficient evidence across species from insects, rodents to humans, demonstrating that the visual system is more sensitive to detecting TP differences in images than other non-TP shape differences, and TP are processed automatically and with higher priority (Chen, 1982, 2005; Chen et al., 2003; Chien et al., 2012; Huang et al., 2018; Todd et al., 1998). Previous evidence from human brain imaging, that is, functional magnetic resonance imaging (fMRI), shows that the inferior temporal cortex (IT) was the main brain area responsible for TP processing (Wang et al., 2007; Zhou et al., 2010; Zhuo et al., 2003). IT is considered to be related to the late stages of processing in the ventral visual stream (Mishkin et al., 1983); thus, the neuroimaging finding seems to conflict with the behavioral evidence of preferential processing of TP. This contradiction leads to a hypothesis that TP is first processed through a fast subcortical pathway and then projected onto the cortical area IT. This subcortical hypothesis of TP processing is supported by evidence from our human brain imaging study that the "hole" of TP is processed in the superior colliculus (SC) and the pulvinar (Meng et al., 2018), and physiological evidence from both humans and mice (Du et al., 2011; Huang et al., 2020; Xu et al., 2018).

The visual system is considered to have two main subsystems, a magnocellular (M) system responsible for the fast processing of coarse information, and a parvocellular (P) system for the slow recognition of details (de Haan & Cowey, 2011; Livingstone & Hubel, 1987). The M pathway is highly sensitive to low luminance contrast while entirely "blind" to chromatic stimuli. The P pathway, by contrast, is color-sensitive with a weak response to low contrast stimuli (Goodale & Milner, 1992; Kaplan & Shapley, 1986). M and P pathways are generally thought to correspond roughly to cortical dorsal "where" and ventral "what" pathways (de Haan & Cowey, 2011; Zhang et al., 2015). In addition to the cortical visual pathways, a small amount of visual information is also processed through the subcortical pathway (Perry & Cowey, 1984; Stepniewska et al., 2000). Physiological evidence shows that neurons in subcortical brain regions such as the amygdala and the superficial layer of the SC also have M characteristics (Kveraga et al., 2007; White et al., 2009; Zhang et al., 2015). Human fMRI studies have suggested that the projections of subcortical M into the higher cortex may be a way to speed up object recognition (Bar et al., 2006). However, it is unclear what exact properties the subcortical M pathway conveys to accelerate visual object processing.

Here, we propose a hypothesis that a subcortical M pathway accelerates object recognition by processing TP first. In the present study, we first demonstrate that TP is rapidly processed via a subcortical M pathway in the early stages of vision, and then show that this early processing of TP is beneficial to rapid object recognition.

There are 64 participants recruited in two experiments. In Exp. 1, we studied the subcortical processing of stimuli by using single-pulse transcranial magnetic stimulation (TMS) over the primary visual cortex (V1) to temporarily block the cortical processing of stimuli. V1 is the first brain region for cortical visual processing. The processing of stimuli is thought to be a cyclic process, and signals in the late stage may re-enter the V1 (Bullier, 2001; Gilbert & Li, 2013; Hupé et al., 1998; Lamme & Roelfsema, 2000). TMS is a noninvasive means of temporarily disrupting neuronal processing (Barker et al., 1985; Hallett, 2000; Kammer, 2007). We applied TMS to V1 at different stimulus onset asynchronies (SOAs). If the early processing of the stimulus occurs in V1, the interference effect of TMS could be observed twice, once in the early feedforward process and once in the late feedback process. We focused on the early processing of stimuli. If TMS at early SOAs does not affect TP discrimination, it suggests that the early processing of TP occurs not in the classical cortical pathway but in a subcortical pathway. In addition, according to the different physiological characteristics of M and P neurons, we designed the M and P stimuli that were preferentially processed in the M and P pathways, respectively. Therefore, in combination with TMS and the M/P stimuli, we were able to investigate whether early processing of TP occurs in a subcortical M visual system. In Exp. 2, we investigated the acceleration effect of this early processing of TP on object perception. Specifically, in an unconscious priming paradigm (Huang et al., 2011), using the M/P stimuli, we examined whether unconscious TP processing in the M pathway can automatically accelerate the discrimination of other properties of objects, such as orientation.

2 | MATERIALS AND METHODS

2.1 | Participants

Sixty-four participants were recruited for the study, including 48 participants in Exp. 1 (16 in Exp. 1A, 1B, and 1C, respectively; 23 males, average age of 22 years) and 16 participants in Exp. 2 (6 males, average age of 22 years). All participants were right-handed and reported normal or corrected-to-normal vision and normal red-green color vision. Participants provided written informed consent, and were paid

to compensate for their time. The study was performed following the tenets of the World Medical Association Declaration of Helsinki and was approved by the Human Research Ethics Committee of the Institute of Biophysics, Chinese Academy of Sciences.

2.2 | Stimuli and procedures

2.2.1 | The M and P stimuli in Exp. 1 and Exp. 2

Visual stimuli were presented on a 19-inch CRT monitor with a 100-Hz refresh rate. According to the response characteristics of M and P system, that is, the M pathway is color blind but sensitive to low-contrast stimuli, while the P pathway is color sensitive but weakly responds to low-contrast stimuli, we designed the stimuli to preferentially engage the M or P pathway, that is, the M or P stimulus. The P stimulus was designed as a green figure on a red background of equal subjective brightness, as illustrated in Figure 1a,c. Compared with the P pathway, the M pathway is selectively activated by low contrast stimuli, e.g., stimulus with below 10% Michelson contrast ($C = (L_{max} - L_{min})/(L_{max} + L_{min})$; Rudvin et al., 2000; Tootell et al., 1988). Thus, the M stimulus was set to a low-contrast, achromatic gray-scale figure.

For the discrimination task in Exp. 1, we controlled the accuracy to be about 70% in order to avoid ceiling and floor effects. The contrast of the M-stimulus for each participant was determined in a preliminary experiment, in which all experimental conditions were included. The mean Michelson contrast of all participants was 6.1% ± 1.4% for about 70% accuracy. For the P stimulus, the luminance of the red and green was subjectively matched for each participant with a minimal flicker procedure, which was used in previous studies (Zhang et al., 2015; Zhang et al., 2016). Red and green square patches flickered at 20 Hz. The red color was fixed. Participants adjusted the green color until the flickering perception was minimized. The adjustment of subjective isoluminance was performed 10 times and the average value was used. Similarly, the task difficulty of the P stimulus also needed to be controlled to be around 70% in Exp. 1. We first selected several values of red with different luminance, and then determined the corresponding green values by the subjective isoluminance procedure, so that we could get some red-green stimulus pairs. Then, a preliminary experiment was conducted to determine the specific pair of red and green stimuli corresponding to 70% accuracy for each participant.

For the priming task in Exp. 2, we mainly investigated the RT index, which required that the stimuli were easy enough to recognize. Therefore, we determined the stimulus conditions corresponding to
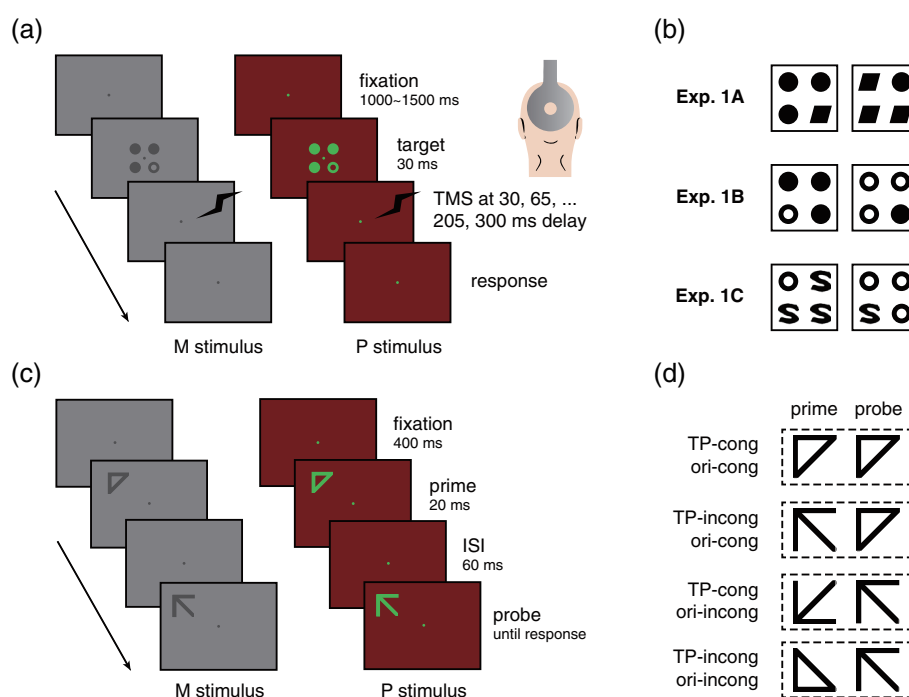

FIGURE 1 Stimulus procedure and examples of Experiments 1 and 2. (a) Stimulus sequence for M and P stimuli in Exp. 1. In each trial, a stimulus array was presented for 30 ms, followed by a single-pulse TMS pulse delivered over the primary visual cortex (V1) at various SOAs after stimulus onset (30, 65, 100, 135, 170, 205, and 300 ms). (b) Stimulus examples of Exp. 1A, 1B, and 1C. The four items comprising the stimuli could be the same, or different in either non-topological properties (TP) shape (non-TP-discrimination, Exp. 1A) or topological property (TP-discrimination, Exp. 1B, 1C). (c) Stimulus sequence for M and P stimuli in Exp. 2. The sequence illustrates a prime-probe pair that is incongruent in TP but congruent in orientation. (d) Examples of four prime-probe congruence conditions. The prime and probe could be one of the four stimuli: 2 TP (one hole, no hole) × 2 orientations (up, down). The triangle (one hole) and arrow (no hole) figures are different in TP. Cong, congruent; incong, incongruent; ori, orientation

the accuracy of about 95% through a preliminary experiment. The M stimulus was fixed to a gray-scale figure with 7.2% Michelson contrast. For the P stimulus, the red value was fixed at RGB [80 0 0] and the green value was also determined by the subjective isoluminance procedure.

2.2.2 | Stimuli in Exp. 1

In Exp. 1, visual stimuli were present in the center region (2° × 2°) of the screen and consisted of four items, each in a quadrant (Figure 1a). Participants reported whether the four items were the same by pressing the left or right arrow keys on the keyboard, with no speed requirement. As illustrated in Figure 1b, the four items could be the same (a 50% chance), or with one item different from the rest either in non-TP properties (i.e., disk vs. parallelogram in Exp. 1A) or in TP (i.e., disk vs. ring in Exp. 1B, and ring vs. S-like figure in Exp. 1C). In the non-TP difference trials of Exp. 1A, there was no difference in area between the items. In the TP difference trials of Exp. 1B, we used geometric figures, i.e., disk and ring, to represent the difference in holes. The sizes of disk and ring items were the same but the areas were different. To avoid the possible confusion of area and other factors in TP change, Exp. 1C used an S-like figure, which matched with the ring in stimulus area and spatial frequency. Stimuli were presented as M or P stimuli in separate blocks, with the order balanced across participants. Each participant completed 448 trials in total. Stimulus presentation and data acquisition were controlled by custom programs written in Matlab (Mathworks, Natick, USA) using Psychtoolbox (Brainard, 1997).

2.2.3 | Procedure in Exp. 1

Participants were required to maintain their fixation throughout a trial, with their heads stabilized in a chin rest at the viewing distance of 57 cm in a dark room. In each trial, a stimulus array was presented for 30 ms, followed by a single-pulse TMS pulse delivered over the V1 at various SOAs (30, 65, 100, 135, 170, 205, and 300 ms). The baseline level at which TMS function essentially disappear was set as the mean performance of the trials with SOAs between 200 and 300 ms (Jolij & Lamme, 2005). D prime (d') value was calculated and used as a measure of the participants' discrimination performance (Macmillan & Creelman, 2004). It is defined as the difference between the z-transforms of hit and false alarm rates, that is, $d' = z(\text{Hit}) - z(\text{False Alarm})$.

2.2.4 | TMS protocol

Single-pulse TMS pulses were delivered over the primary visual cortex using a Magstim 200 (Whiland, UK) stimulator and a 140-mm circular TMS coil. The circular coil was placed tangentially on the skull, with the handle held upward. For localization, the lower rim of circular coil was initially positioned 1.5 cm above the inion (over the occipital pole). Participants were required to maintain fixation at the center of the screen (black background) and report the position of phosphene in the visual field if any. The coil was then moved around in small steps and single pulses of TMS were applied until a clear phosphene was perceived in the central visual field covering visual stimuli (about 2°). After the TMS localization, we assessed the TMS intensity at which participants would perceive phosphene in half of 10 trials (i.e., phosphene threshold) using a staircase procedure (Herring et al., 2015; Kammer et al., 2005). TMS intensity was initially set at 60% of maximal stimulator output, and then was increased in steps of 5% per TMS pulse until the participant reported seeing a phosphene. Trains of 10 pulses were applied and the percentage of trials in which a phosphene was perceived was calculated. The TMS intensity was then decreased (phosphene trials percentage > 50%) or increased (phosphene trials percentage < 50%) by 1%, until the phosphene threshold was found. The TMS intensity during the experiment was set for each participant at 100% of the phosphene threshold (about 62% ± 6% of maximal stimulator output on average).

2.2.5 | Stimuli and procedures in Exp. 2

In each trial of Exp. 2 (see Figure 1c), a 20-ms prime stimulus was followed by a probe stimulus with an inter-stimulus interval (ISI) of 60 ms. The prime (1.13°) and probe (1.88°) stimuli were presented at one of four quadrants of the screen with their centers at an eccentricity of 5.6°. The prime and probe stimuli could be arrows or triangles with various orientations (e.g., "◁↑", "◸↑"). We manipulated the congruence of prime and probe stimuli in TP (hole vs. no-hole) and orientation (up vs. down). The prime and probe stimuli could have one of two possible TP (one hole or no hole) and one of two orientations (up or down), yielding the following prime-probe congruence pairs as illustrated in Figure 1d: congruent in both properties (TP-congruent and orientation-congruent), incongruent in TP but congruent in orientation (TP-incongruent and orientation-congruent), congruent in TP but not in orientation (TP-congruent and orientation-incongruent), and incongruent in both properties (TP-incongruent and orientation-incongruent). Participants reported TP and orientation of the probe in separate blocks. The probe was presented until a response was given. The response time (RT) in each trial was calculated from the onset of the probe stimulus. Stimuli were also presented as M or P stimuli in separate blocks. Each participant completed 768 trials in total, with 192 trials in each of the four blocks (2 tasks: TP or orientation × 2 M/P stimuli).

3 | RESULTS

3.1 | The subcortical M visual system is engaged in the early processing of TP

In Exp. 1, we tested whether early processing of TP occurs in a subcortical M visual system. The stimuli were designed to bias M

or P processing. We used single-pulse TMS on the V1 to temporarily block cortical processing of M or P stimuli at different SOAs after stimulus onset (from 30 ms to 300 ms). If the early processing of TP is independent of the early visual cortex, then it should be unaffected when the V1 function is temporarily disrupted at the early SOAs. As shown in Figure 2, these 'dips' on the curves represent a disruption of task performance. The first dip around 30 ms is considered to reflect a disruption of the early feedforward processing, while the latter dip around 135–170 ms represents an interruption of the feedback processing from higher cortical areas to V1.

A two-way analysis of variance (ANOVA) with SOAs and M/P stimuli as factors was conducted on d' values of Exp. 1A, B, and C, respectively. Detailed statistical results are presented in Table 1. For the three experiments, the main effects of SOA were all significant ($ps < .05$), suggesting that TMS at different times had different effects on performance. The main effects of M/P stimuli were not significant ($ps > .1$), suggesting similar task difficulty for M and P stimuli. For the TP-discrimination condition, the interaction between the two factors was marginally significant ($p = .076$, Exp. 1B) or significant ($p = .025$, Exp. 1C), suggesting that TMS had different effects between M and P conditions. In contrast, non-significant interaction ($p = .813$) in
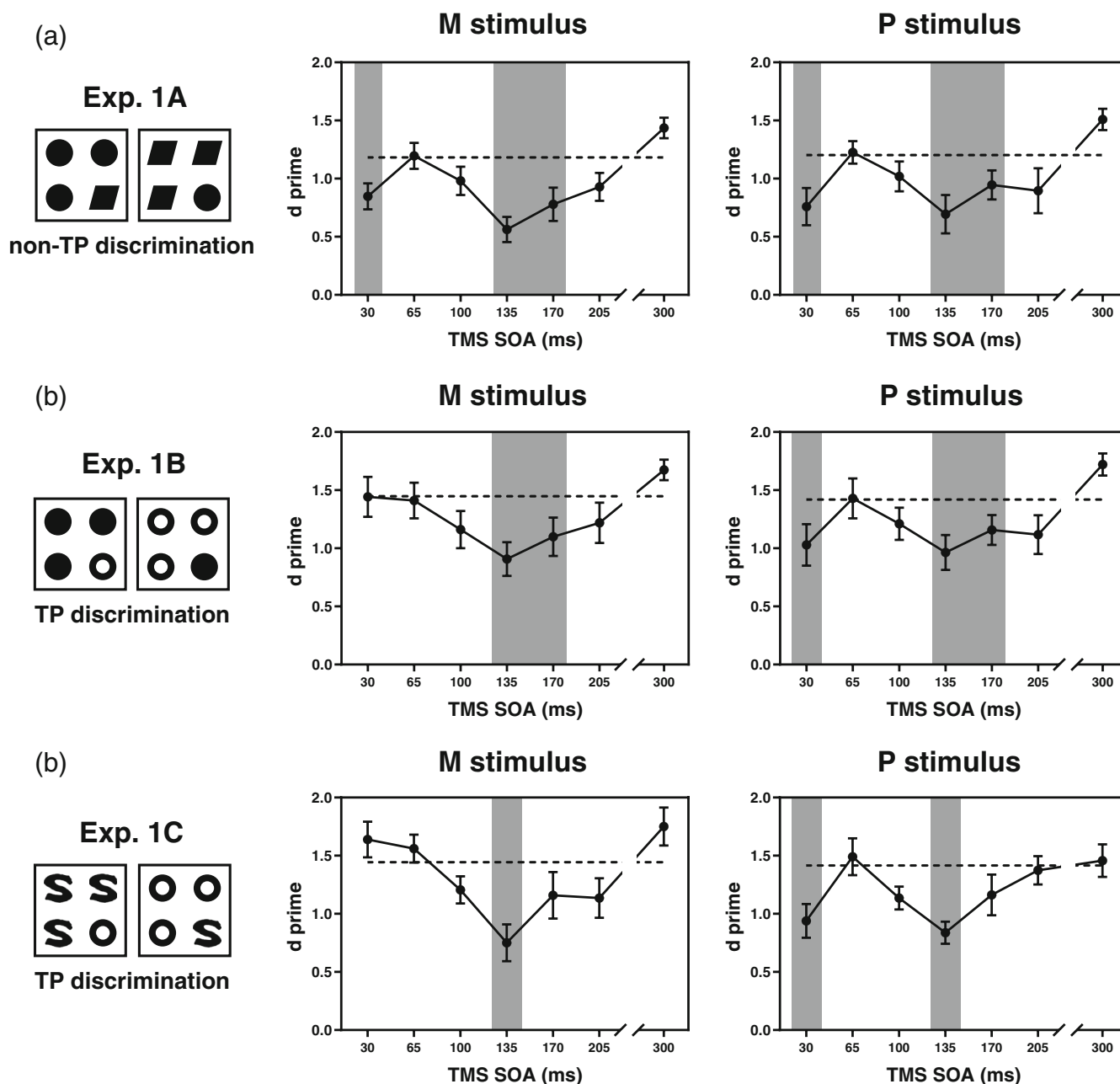

FIGURE 2 Performance of non-topological properties (TP) and TP discrimination in experiments 1A, B, and C. The discrimination performance (d' value) is given at each TMS SOA. The shaded columns indicate the time window of significant decline of discrimination performance ($p < .05$) compared with the baseline (dash line, average d' value at 200–300 ms SOAs)

ANOVA factors	Exp. 1A	Exp. 1B	Exp. 1C
M/P stimuli			
F	0.07	0.03	0.34
p	.798	.866	.568
η_p^2	.005	.002	.02
SOA			
F	8.86	3.21	12.51
p	<.001***	.019*	<.001***
η_p^2	.37	.18	.46
M/P × SOA			
F	0.39	2.23	2.99
p	.813	.076	.025*
η_p^2	.03	.13	.17

Note: A two-way ANOVA with SOAs and M/P stimuli as factors was conducted on d' values of Exp. 1A, B, and C, respectively. Effect sizes are expressed as η_p^2.
*p < .05; ***p < .001.

Exp. 1A indicated that for the non-TP discrimination the effect of TMS was similar between M and P conditions.

The baseline was set as the average of d' values at 205 and 300 ms SOAs. There were no significant differences between any of the six baselines (all ps > .2). Then, d' values at TMS SOAs of 30, 65, 100, 135, and 170 ms were compared with the baseline for M and P stimuli, respectively. See Table 2 for detailed statistics. For both M and P stimuli in the non-TP-discrimination condition (Exp. 1A), d' values at 30, 135, and 170 ms SOAs were significantly below the baseline (ps < .05). The results of Exp. 1A suggest that TMS disruption of V1 significantly reduced non-TP-discrimination performance at the stages of both feedforward and feedback processing. In the TP-discrimination condition (Exp. 1B and C), the drop in performance was different for M and P stimuli. For P stimuli, both early (30 ms) and late dips (135–170 ms) existed. However, for M stimuli, only the late dip existed whereas the early dip disappeared, suggesting that the early feedforward processing of TP in the M pathway is not affected by TMS on V1. That is, the early processing of TP is not in the classical cortical pathway but in a subcortical pathway. In contrast, P-biased TP processing is similar to non-TP processing in that their early feedforward processes both occur in the V1.

3.2 | Unconscious TP processing through the M pathway accelerates object recognition

A previous study, using the unconscious priming paradigm, has found that TP congruence between unconscious prime and target stimuli could accelerate perception of other properties, such as orientation and color, regardless of whether the task is TP relevant or irrelevant (Huang et al., 2011), suggesting that TP processing can automatically

speed up object recognition. In Exp. 2, we combined the unconscious priming paradigm with M/P stimuli to examine whether this TP facilitation effect on object recognition occurs only in the M pathway. As shown in Figure 1d, we manipulated the congruence of prime and probe stimuli in TP (hole vs. no-hole) and orientation (up vs. down). Participants performed well in all four blocks (2 tasks: TP or orientation × 2 M/P stimuli), with an average accuracy of 97%. The RTs were submitted into a four-way ANOVA with tasks, M/P stimuli, TP congruence, and orientation congruence as within-subject factors. Detailed statistical results are presented in Table 3. We found that RTs were shorter for the TP task than for the orientation task (p < .001) and priming effects (RT of incongruent–RT of congruent) were robust for both TP and orientation congruence, i.e., RTs were shorter for prime-probe congruent pairs than for incongruent ones (ps < .01). The mean RT for M stimuli was not different from that for P stimuli (p = .662), suggesting that similar task difficult for M and P stimuli. Significant interactions between tasks and either type of congruence suggest that task relevance affected priming effects.

Due to the significant interactions and the purpose of the study to test whether the priming effect of TP mainly occurs in the M pathway, we performed further posthoc analyses with Holm correction to examine the priming effects in different tasks and M/P conditions. Detailed statistical results are shown in Table 4. We found that the priming effect of TP was significant in both tasks only when the stimuli were biased toward M pathway processing, but disappeared with P-biased stimuli (see Figure 3). In contrast, the priming effect of orientation only occurred when orientation was reported and when the stimuli were biased toward P pathway processing. The finding of the facilitation effect of TP congruence on both TP and non-TP (e.g., orientation) perception is consistent with our previous work (Huang et al., 2011). Critically, in this study, we found that this facilitation effect of TP congruence was restricted to the M visual system. That is, the early processing of TP in the M pathway, not in the P pathway, accelerates object recognition.

To make sure unconsciousness of the priming effect, we tested the visibility of prime stimuli in another four experimental blocks (2 tasks: TP or orientation × 2 M/P stimuli). The accuracy rates for reporting primes in the four blocks were not different from the chance level of 50% (all ps > .167), indicating that both TP and orientation of the prime stimuli were invisible with either M or P stimuli.

4 | DISCUSSION

The visual system may achieve fast object recognition by extracting TP of objects. However, the mechanism of how TP is rapidly processed and how it affects object recognition is still unclear. Experiment 1 investigated the subcortical M hypothesis of TP processing by applying TMS to temporarily block the processing of the cortex. We found that TMS disruption of V1 significantly reduced non-TP-discrimination performance at the stages of both early (feedforward) and late (feedback) processing. By contrast, the early processing of TP in the M pathway escaped the effect of TMS, suggesting that the

TABLE 2 Statistical results of paired *t*-tests in Experiments 1A, B, and C

| Experiment	M/P	SOA (ms)	*t*	*p*	*p* FDR	Cohen's *d*
Exp. 1A	M stimulus	30	−2.36	.032*	.054	−.59
		65	0.08	.938	.938	.02
		100	−1.71	.108	.135	−.43
		135	−5.50	<.001***	<.001***	−1.38
		170	−2.76	.015*	.036*	−.69
	P stimulus	30	−3.68	.002**	.011*	−.92
		65	0.18	.862	.862	.04
		100	−1.14	.271	.339	−.29
		135	−3.36	.004**	.011*	−.84
		170	−2.23	.041*	.069	−.56
Exp. 1B	M stimulus	30	−0.03	.977	.977	−.007
		65	−0.27	.795	.977	−.07
		100	−1.57	.137	.228	−.39
		135	−3.83	.002**	.008**	−.96
		170	−2.61	.020*	.049*	−.65
	P stimulus	30	−3.80	.002**	.004**	−.95
		65	0.09	.932	.932	.02
		100	−1.76	.100	.125	−.44
		135	−3.92	.001**	.004**	−.98
		170	−2.34	.033*	.056	−.59
Exp. 1C	M stimulus	30	1.28	.220	.275	.32
		65	0.65	.528	.528	.16
		100	−1.34	.201	275	−.34
		135	−3.28	.005**	.025*	−.82
		170	−1.40	.182	.275	−.35
	P stimulus	30	−4.20	<.001***	.002**	−1.05
		65	0.50	.622	.622	.13
		100	−1.96	.068	.114	−.49
		135	−4.93	<.001***	<.001***	−1.23
		170	−1.18	.255	.319	−.30

Note: We compared *d*′ values at TMS SOAs of 30, 65, 100, 135, and 170 ms with the baseline (average *d*′ at 205 and 300 ms SOAs) for M and P stimuli, respectively. Effect sizes are expressed as Cohen's *d*.
*p < .05; **p < .01; ***p < .001.

early processing of TP is independent of the visual cortex, but through a subcortical M pathway. Further, under the unconscious priming paradigm of Experiment 2, we found that the processing of TP in the subcortical M pathway automatically accelerated the perception of other properties.

4.1 | Possible confounding factors related to topological changes were controlled

Topological changes may result in changes in stimulus area and spatial frequency (e.g., the disk and ring stimuli in Exp. 1B), so we specifically balance these possible confounding factors. For example, the stimulus pair 'S' and 'O' in Exp. 1C were matched in stimulus area and spatial

frequency, and so were the arrow and triangle stimuli (e.g., "△" and "↗") in Exp. 2. Although "S" and "O" pairs match in physical attributes, there may be some interference factors such as semantic differences. The geometric stimuli such as disk and ring pairs in Exp. 1B can avoid semantic differences. In a word, we have controlled for possible confounding factors related to topological changes.

4.2 | The subcortical M visual system is engaged in the early processing of TP

The present study applied TMS to V1 at different SOAs, allowing us to track the time course of the functional relevance of the early visual cortex. Invasive recording in humans indicates that the earliest activity

TABLE 3 Statistical results of four-way ANOVA of response times (RTs) in Experiment 2

Four-way ANOVA	F	p	η_p^2
Tasks	25.31	<.001***	.63
M/P stimuli	0.20	.662	.01
TP cong	12.37	.003**	.45
Ori cong	10.69	.005**	.42
Tasks × M/P stimuli	8.75	.01*	.37
Tasks × TP cong	6.16	.025*	.29
Tasks × Ori cong	11.27	.004**	.43
M/P stimuli × TP cong	28.98	<.001***	.66
M/P stimuli × Ori cong	2.09	.169	.12
TP cong × Ori cong	3.02	.103	.17
Tasks × M/P stimuli × TP cong	0.08	.784	.005
Tasks × M/P stimuli × Ori cong	1.35	.263	.08
Tasks × TP cong × Ori cong	0.06	.808	.004
M/P stimuli × TP cong × Ori cong	0.08	.786	.005
Tasks × M/P stimuli × TP cong × Ori cong	0.87	.366	.06

Note: Tasks, M/P stimuli, topological properties (TP) congruence, and orientation congruence serve as within-subject factors. Effect sizes are expressed as η_p^2. Cong, congruence; ori, orientation.
*p < .05; **p < .01; ***p < .001.

TABLE 4 Statistical results of priming effects in Experiment 2 (Holm correction)

Task	M/P	Priming effect	t	p	Cohen's d
TP	M stimulus	TP	5.39	<.001***	.49
		Orientation	−0.21	1	−.02
	P stimulus	TP	1.03	1	.09
		Orientation	.53	1	.05
Orientation	M stimulus	TP	3.15	.049*	.29
		Orientation	2.05	.391	.19
	P stimulus	TP	−0.59	1	−.05
		Orientation	4.64	<.001***	.44

*p < .05; ***p < .001.

in V1 starts about 30 ms after stimulus onset (Wilson et al., 1983). The first TMS dip around 20–40 ms is considered to reflect the disruption of early feedforward processing in V1 (de Graaf et al., 2014). Our finding of the lack of a first TMS dip around 30 ms when TP processing is biased to the M pathway suggests that the early processing of TP is not affected by TMS disruption of V1. In other words, the early stage of TP processing in the M pathway does not occur in the cortex but in a subcortical M pathway. In contrast, the early processing of TP in the P pathway is severely disrupted by TMS, suggesting that the processing of the P pathway takes place in the cortex. These findings suggest that early fast processing of TP occurs in a subcortical M pathway and that the subcortical visual pathway is primarily an M pathway, which is consistent with previous studies (Kveraga et al., 2007; Zhang et al., 2015).

A classical subcortical pathway, SC-Pulvinar-Amygdala, is considered to be responsible for the fast processing of "critical" visual information (McFadyen et al., 2019; Morris et al., 1999; Rafal et al., 2015).

For example, when mice are exposed to a threatening looming stimulus that mimics flying eagles, they demonstrate defensive flight-to-nest behavior, which is considered to be mediated by the subcortical pathway (Shang et al., 2015). Interestingly, our recent work on mice (Huang et al., 2020) shows that a topological change in the looming stimulus weakened the defensive responses and reduced cell activation in the SC, which suggests that the detection of threatening information is dependent on TP-based object representations. In addition, a recent human fMRI study has functionally identified this subcortical pathway as being involved in negative emotional processing (Kragel et al., 2021). Meng et al. (2012) have found that fear emotion would interfere with topological perception and this interference is associated with common neural correlation in the amygdala. In summary, the above evidence suggests that TP and threatening/negative information processing may co-occur in the subcortical pathway. The present findings from the TMS study provide human evidence for the involvement of a subcortical M pathway in TP processing. In other

FIGURE 3 Priming effects and response times (RTs) in experiment 2. (a) Priming effects (RT of incongruent − RT of congruent) of topological properties (TP) and orientation. TP congruence speeded up reports of both TP and orientation, while orientation congruence only accelerated orientation judgment. Moreover, the priming effect of TP was found only when the stimuli were biased toward M pathway processing, while the priming effect of orientation occurred only when the stimuli were biased toward P pathway processing. (b) RTs of reporting TP (left) or orientation (right) in conditions of M and P stimuli. *p < .05; ***p < .001. Error bars represent the standard errors of the means
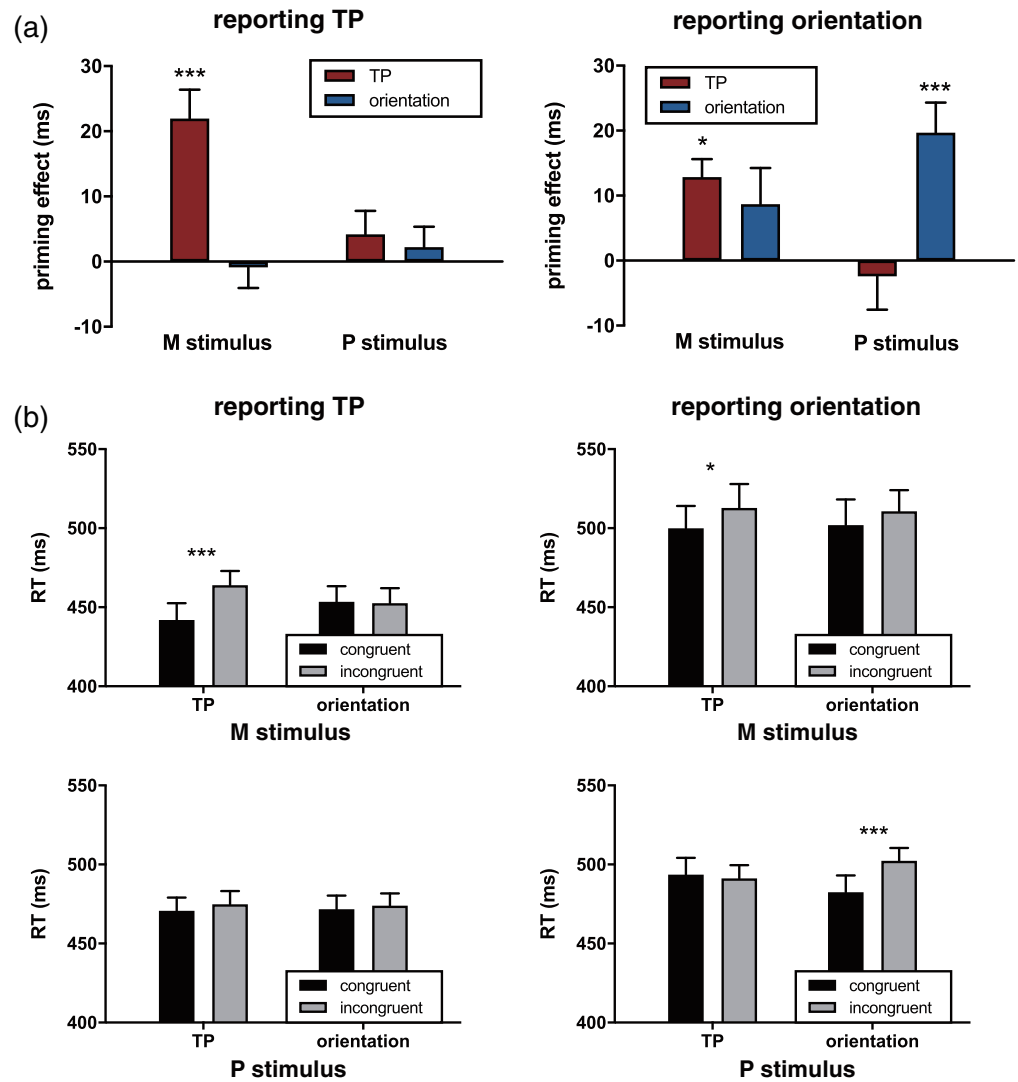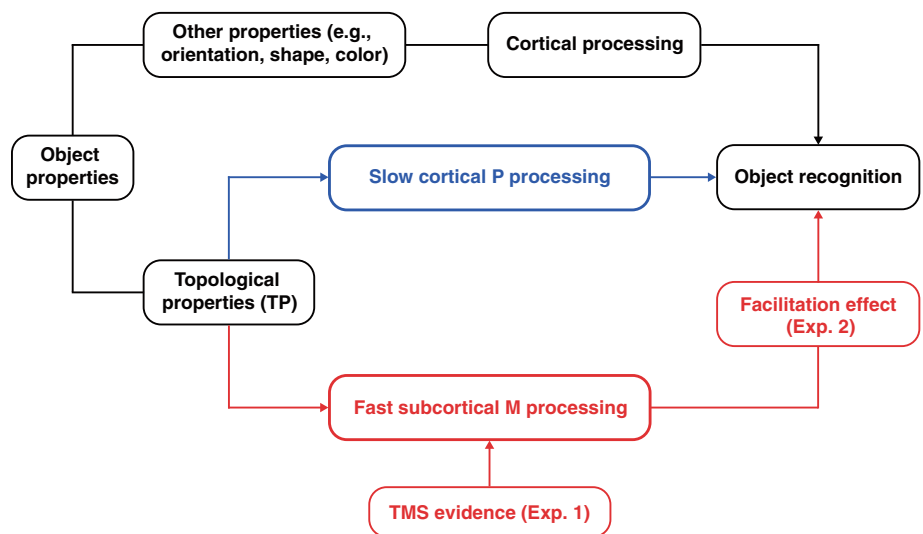
FIGURE 4 Schematic of the subcortical processing of topological properties (TP) and its facilitation effect of object recognition

words, the subcortical pathway plays a key role in the establishment of early object representation, which could be a newly discovered function of the conservative subcortical visual system. And this new function has implications for further understanding of the mechanisms of subcortical-dysfunction-related diseases, such as schizophrenia and glaucoma (Shen et al., 2021; Sun et al., 2019; Zhang et al., 2016).

Future work to identify and characterize neural circuits involved in subcortical topological perception may help understand and treat these disorders.

4.3 | Unconscious TP processing through the M pathway accelerates object recognition

In Exp. 2, we investigated whether a subcortical M pathway contributes to the fast object recognition by extracting TP of objects. Firstly, the findings of Experiment 2 repeated the facilitation effect of unconscious topological processing on objects' feature recognition (Huang et al., 2011). And TP priority effect was also observed, manifested by a shorter RT for the TP report than for the orientation report. More importantly, we found that this TP facilitation effect critically depended on the processing of the M pathway, and disappeared when the stimulus was biased toward P pathway processing. The findings suggest that the visual system facilitates object recognition by prioritizing TP in the fast M pathway. In addition, previous fMRI studies showed that TP processing in the cortex mainly occurred in the ventral pathway corresponding to the P pathway, but not in the dorsal pathway corresponding to the M pathway (Wang et al., 2007; Zhou et al., 2010; Zhuo et al., 2003). Together with the task-irrelevant and unconscious condition of Exp. 2, it can be inferred that TP processing via the M pathway occurs in the subcortical pathway rather than the cortical pathway.

Kveraga et al. (2007) have proposed that a subcortical M pathway may be responsible for fast object recognition by carrying low spatial frequencies. The subcortical pathway indeed exhibits a preference for conveying the low spatial frequency components. For instance, the neurons in the SC responded optimally to gratings of low spatial frequencies and showed a narrow spatial frequency tuning (Márkus et al., 2009). Some fMRI studies also found greater activation of low spatial frequency fearful faces in the SC, pulvinar, and amygdala (McFadyen et al., 2017; Vuilleumier et al., 2003). We do not deny the role of low spatial frequencies in rapid object recognition. Our study finds that topological processing by the subcortical M pathway accelerates object recognition even after controlling for spatial frequency. This finding contributes to the fast object recognition mechanism of the subcortical M pathway.

According to the topological theory proposed by Chen (1982) and Chen (2005), the visual system first automatically extracts TP to build a representation of an object and then assigns other properties to the object (Figure 4). When a prime stimulus appears, an initial object representation is built based on TP. If the following probe stimulus has the same TP as the prime stimulus, the existing object representation will be used. If not, there will be a new object representation to be constructed, which will cost extra response times. Therefore, TP congruence between prime and probe stimuli accelerates object processing, regardless of what property is to report.

5 | CONCLUSIONS

The present study provides TMS evidence that a subcortical M pathway is responsible for the early processing of TP and this subcortical processing of TP accelerates object recognition. The current findings shed light on a new function of the subcortical pathway, that is, involved in the early processing of shape perception of objects.

AUTHOR CONTRIBUTIONS
Wengbo Wang: Data curation, Formal analysis, Writing—original draft, Visualization. **Tiangang Zhou:** Methodology. **Lin Chen:** Supervision, Project administration. **Yan Huang:** Conceptualization, Methodology, Data curation, Formal analysis, Supervision, Project administration, Writing - review & editing.

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