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BRIEF REPORT

Causal Evidence for Adaptive Recruitment of Subcortical and Cortical Pathways in Rapid Fear Processing

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This study addresses the long-standing debate on whether the subcortical or cortical visual pathway underlies rapid transmission of threat-related information. Using a single-pulse transcranial magnetic stimulation protocol to transiently disrupt V1/V2 function at various time points, we examined the necessity of early visual cortices at different phases of fear processing. Our results showed that early disruption of V1/V2 had no effect on fearful emotion recognition under conditions of limited visual accessibility ($N = 28$ adults), but significantly impaired fear recognition when visual accessibility was increased ($N = 28$ adults). Notably, the impairment occurred as early as 30 ms poststimulus onset and was specific to low spatial frequency information, in stark contrast to the impairment on nonaffective content of the stimuli. These findings suggest a dual-pathway system in the human brain that flexibly engages either the subcortical or cortical pathway, depending on the availability of threat information in the environment.

Keywords: transcranial magnetic stimulation, fear processing, subcortical pathway, cortical pathway, low spatial frequency

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The prioritized processing of threatening emotions has been explained by a subcortical pathway model, which proposes that threat signals are transmitted to the amygdala via the colliculus–pulvinar pathway, bypassing the presumably slower and resource-dependent processing in the visual cortex (LeDoux, 1996). This model is supported by evidence of rapid, preconscious processing of threat-related information (Inagaki et al., 2023; Méndez-Bértolo et al., 2016; Sato et al., 2011; Y. Wang, Luo, et al., 2023), which exhibits functional characteristics of the implicated brain structures in the subcortical pathway (Méndez-Bértolo et al., 2016; Vuilleumier et al., 2003; Yu et al., 2024). However, these effects are also compatible with an alternative cortical pathway model, which suggests the presence of short-cut cortical routes that allow for rapid transmission of threat information within the cortex (Pessoa & Adolphs, 2010). As such, existing evidence does not definitively distinguish between the subcortical and cortical pathway models. It remains unclear whether one pathway predominates or if both pathways can coexist.

Given the extensive interconnections between the subcortical and cortical pathways (Tamietto & de Gelder, 2010), we hypothesize that the two pathways may coexist. However, as the cortical and subcortical structures often play competing roles in emotion processing (Tamietto et al., 2012), their engagement may depend on distinct conditions. Specifically, the subcortical structures are preferentially sensitive to subliminal compared to supraliminal stimuli (Brooks et al., 2012; Diano et al., 2017; F. Guo et al., 2024), while cortical structures are more responsive to supraliminal stimuli (Fang & He, 2005;

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Jolij & Lamme, 2005). Based on this distinction, we hypothesize that the recruitment of each pathway adaptively depends on the availability of visual information in the environment.

To test these hypotheses, we employed a single-pulse transcranial magnetic stimulation (TMS) protocol to causally disrupt the function of V1/V2 (de Graaf et al., 2014) at various time intervals following brief (16.7 ms, Experiment 1) or extended (33.3 ms, Experiment 2) presentation of fearful and neutral faces (Pessoa et al., 2005). To ensure that the TMS effects were specific to prioritized fear processing, we implemented three critical controls. First, TMS pulses were administered at one of seven stimulus-onset synchronies (SOAs)—30, 60, 90, 120, 150, 210, and 270 ms—with specific SOAs designated for disrupting either rapid feedforward transmission (30 and 60 ms), later-phase feedback transmission (90, 120, and 150 ms), or serving as control conditions with no TMS influence (210 and 270 ms; Jolij & Lamme, 2005). Second, the faces were low-spatial-frequency (LSF) and high-spatial-frequency (HSF) filtered to isolate specific processing of coarse versus fine visual information. Third, in addition to emotion recognition, a gender recognition task was involved in Experiment 2 to verify functional dissociations between the TMS effects on emotion and nonemotion processes. Given that prioritized fear processing in the amygdala occurs within 90 ms and is particularly responsive to LSF visual information (Burra et al., 2019; Inagaki et al., 2023; Méndez-Bértolo et al., 2016; Y. Wang, Luo, et al., 2023), we predicted that if rapid fear transmission occurs via the cortical pathway, TMS disruption of V1/V2 would impair fear recognition for LSF stimuli within this timeframe. Otherwise, rapid processing of coarse fear is likely mediated by the subcortical pathway.

Method

Participants

Twenty-eight adults took part in each experiment (Experiment 1: five men, $M_{\text{age}} = 21.63$ years; Experiment 2: four men, $M_{\text{age}} = 21.18$ years). Due to the absence of directly comparable paradigms, the sample size was determined based on prior research investigating prioritized fear processing under similar experimental conditions (Yu et al., 2024). All participants provided written informed consent prior to participation. The experimental procedures were approved by the Human Subject Review Committee of Zhejiang University.

Transparency and Openness

All data and analysis code have been made publicly available and can be accessed at https://osf.io/8BJNR/ (J. Guo et al., 2025).

Stimuli

Visual stimuli were presented on a liquid-crystal display screen with a 60-Hz refresh rate. The stimuli were face images from 24 actors (12 females) displaying fearful and neutral emotions, selected from the NimStim Set of Facial Expressions (https://danlab.psychology.columbia.edu/content/nimstim-set-facial-expressions). All images were gray-scaled, cropped to minimize hair and background distractions, and standardized to a size of 2° × 2.54° with equal mean luminance (Y. Wang, Luo, et al., 2023). To manipulate spatial frequency, the original face images were filtered using a low-pass cutoff of <6 cycles per image (LSF) and a high-pass cutoff of >24 cycles per image (HSF). Each experiment utilized 96 images, representing two emotions, two genders, and two spatial frequency conditions.

Procedure

Experiment 1

Each trial started with a 500-ms fixation, followed by a face displayed at the center of the screen for 16.7 ms. A single-pulse TMS was then delivered over V1/V2 at one of seven SOAs: 30, 60, 90, 120, 150, 210, and 270 ms. Participants were required to judge the face's emotion (fearful or neutral) as accurately and quickly as possible, with a response time limit of 2,000 ms (Figure 1A).

Experiment 2

The procedure was identical to Experiment 1, with two key modifications. First, the face presentation duration was extended to 33.3 ms. Second, an additional gender discrimination task was included (Figure 1A). Participants judged both the emotion (fearful or neutral) and gender (female or male) of each face, with the order of tasks counterbalanced across participants.

In both experiments, the order of trials was randomized with respect to SOA, emotion, gender, and spatial frequency. Participants completed a total of 672 trials, divided into four blocks.

TMS Protocol

Single-pulse TMS was administered to V1/V2 using a PowerMAG 100 (MAG & More GmbH, Germany) stimulator with a 140-mm figure-eight coil. V1/V2 localization was achieved through a functional method in which the TMS stimulation elicits phosphenes that intrude on the center of the visual field where the target stimuli were to be displayed. The midpoint of the coil was initially positioned 1.5–2 cm dorsal from the inion, and participants were instructed to fixate on a central point on the screen while reporting any phosphene perception. The coil position was then systematically adjusted in small steps until clear, reliable phosphenes were reported (Laycock et al., 2007). A screening procedure was applied that excluded participants who could not report phosphenes from participating in the formal experiment.

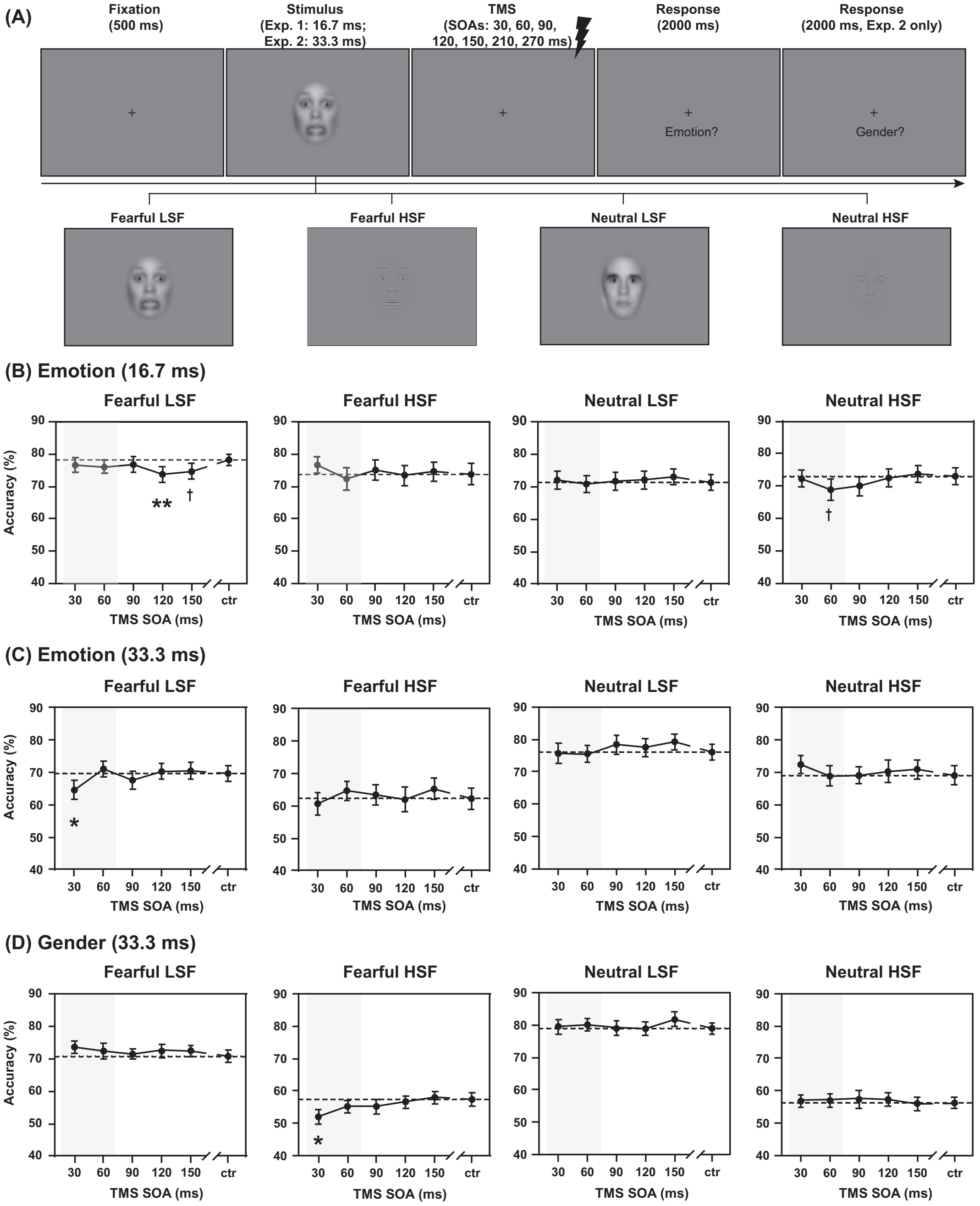
To determine the TMS stimulation intensity, each participant's phosphene threshold was measured using a staircase procedure (Herring et al., 2015; W. Wang, Zhou, et al., 2023). The initial TMS intensity was set at 65% of the maximal stimulator output and adjusted in steps of 5% decrements or 2% increments until participants reported phosphenes in five out of 10 pulses. The final stimulation intensity was set at 120% of the phosphene threshold. On average, the TMS intensity was 61% of the maximal stimulator output in Experiment 1 and 58% in Experiment 2.

Data Analysis

Trials with no response were excluded from the data analysis (0.35% in Experiment 1; 0.31% for emotion recognition and 0.37% for gender recognition in Experiment 2). Paired-sample *t* tests were conducted to compare the recognition accuracy for each emotion

Figure 1

Experimental Procedure and Results



Note. (A) Participants were tasked with recognizing the emotion (and gender, in Experiment 2) of briefly presented fearful or neutral faces filtered to contain only LSF or HSF information, while single-pulse TMS was applied over V1/V2 at different SOAs. Example images of LSF and HSF fearful and neutral faces are shown at the bottom. (B) Impaired fear recognition was not observed at early SOAs when faces were presented for 16.7 ms. Recognition deficits were observed for LSF fearful faces at the 120-ms and 150-ms SOAs and for HSF neutral faces at the 60-ms SOA. (C) When faces were presented for 33.3 ms, impaired emotion recognition was observed for LSF fearful faces at the 30-ms SOA. (D) Impaired gender recognition was observed for HSF fearful faces at the 30-ms SOA when faces were presented for 33.3 ms. Dotted lines represent recognition accuracies in the control (ctr) condition. Shaded areas indicate early TMS SOAs designated for disrupting rapid feedforward transmission. LSF = low spatial frequency; HSF = high spatial frequency; TMS = transcranial magnetic stimulation; SOAs = stimulus-onset asynchronies; Exp. = experiment. The faces used in Figure 1A were obtained from the NimStim Set of Facial Expressions (Tottenham et al., 2009), which allows free usage of the faces for scientific research purpose.

$^{\dagger} p_{\text{uncorrected}} < .05, \quad p_{\text{Bonferroni}} < .10. \quad ^{*} p_{\text{Bonferroni}} < .05. \quad ^{**} p_{\text{Bonferroni}} < .01.$

(fearful and neutral) and spatial frequency (LSF and HSF) condition at each target SOA (30, 60, 90, 120, and 150 ms) with that in the control condition (mean accuracy of 210- and 270-ms SOAs). Given our a priori hypothesis that TMS disruption would reduce performance, a one-tailed α level of .05 was applied. To account for the multiple comparisons, Bonferroni correction was used. Additionally, Bayes factors were calculated for all t tests using the Bayesian methods module in *jamovi* software (Version 2.3.28). Statistics for each comparison are detailed in the Supplemental Tables.

Results

Experiment 1: Independence of Early Visual Cortex Under Limited Visual Accessibility

We first focused our analysis on the feedforward process at 30- and 60-ms SOAs. We found that TMS disruption of V1/V2 only weakly impaired recognition of HSF neutral faces (Figure 1B), $t(27) = -2.18$, $p_{\text{Bonferroni}} = .095$, Cohen's $d = -0.41$, $\text{BF}_{10} = 2.99$, at the 60-ms SOA, consistent with the reliance of HSF information processing on cortical visual pathways. No recognition deficits were found at the 30-ms SOA for any emotion and spatial frequency combinations ($ps_{\text{Bonferroni}} \geq .970$). Critically, LSF fear recognition remained unaffected at the 60-ms, $t(27) = -1.57$, $p_{\text{Bonferroni}} = .320$, Cohen's $d = -0.30$, $\text{BF}_{10} = 1.12$, and 30-ms, $t(27) = -0.88$, $p_{\text{Bonferroni}} = .970$, Cohen's $d = -0.17$, $\text{BF}_{10} = 0.45$, SOAs. These results suggest that rapid processing of brief fear operates independently of early visual cortex involvement.

While TMS on V1/V2 did not impair rapid fear processing at early SOAs, we observed impaired recognition of LSF fear at later SOAs of 120 ms, $t(27) = -3.30$, $p_{\text{Bonferroni}} = .005$, Cohen's $d = -0.62$, $\text{BF}_{10} = 27.90$, and 150 ms, $t(27) = -2.15$, $p_{\text{Bonferroni}} = .100$, Cohen's $d = -0.41$, $\text{BF}_{10} = 2.84$. These findings suggested a critical role for the cortical pathway in fear recognition, likely in the feedback phase.

Experiment 2: Dependence of Early Visual Cortex Under Higher Visual Accessibility

To encourage engagement of the cortical pathway, Experiment 2 extended stimulus duration to 33.3 ms. A gender discrimination task known to rely more on the cortical pathway was also included to further assess cortical involvement (Haxby et al., 2000). In contrast to Experiment 1, we observed a significant decrease in emotion recognition for LSF fearful faces at the 30-ms SOA (Figure 1C), $t(27) = -2.97$, $p_{\text{Bonferroni}} = .015$, Cohen's $d = -0.56$, $\text{BF}_{10} = 13.80$, indicating early cortical involvement in LSF fear processing. In line with existing evidence that rapid fear processing is specific to LSF content, this impairment was not found in HSF fear recognition, $t(27) = -0.84$, $p_{\text{Bonferroni}} = 1.000$, Cohen's $d = -0.16$, $\text{BF}_{10} = 0.43$, or LSF/HSF neutral emotion recognition ($ps_{\text{Bonferroni}} = 1.000$) at the same SOA. No emotion recognition impairments were detected at the 60-ms SOA ($ps_{\text{Bonferroni}} = 1.000$). Therefore, rapid fear processing is supported by the cortical visual pathway in this context.

The inclusion of the gender discrimination task further highlighted the adaptive nature of the cortical pathway. Specifically, consistent with the notion that gender processing depends more on HSF information and cortical pathways than emotion processing, early disruption of cortical functions at the 30-ms SOA no longer disrupted emotion recognition of HSF faces (Figure 1D, $ps_{\text{Bonferroni}} = 1.000$). Instead, it selectively impaired gender recognition of HSF faces, $t(27) = -2.64$, $p_{\text{Bonferroni}} = .035$, Cohen's $d = -0.50$, $\text{BF}_{10} = 8.79$. Thus, the cortical visual pathway is adaptively engaged in tasks in which it is primarily involved.

To further confirm that the spatial frequency-specific impairment in emotion and gender recognition resulted from increased visual accessibility rather than heightened task difficulty due to the additional task in Experiment 2, we split participants into two groups based on their overall emotion and gender recognition accuracy in the control condition (Supplemental Figure S1). Significant impairments in LSF fear recognition, $t(13) = -3.02$, $p_{\text{Bonferroni}} = .025$, Cohen's $d = -0.81$, $\text{BF}_{10} = 11.50$, and HSF gender recognition, $t(13) = -4.98$, $p_{\text{Bonferroni}} < .001$, Cohen's $d = -1.33$, $\text{BF}_{10} = 255.04$, were observed at 30-ms SOA only in the high-accuracy group, which likely experienced higher visual accessibility but lower task difficulty. In contrast, the low-accuracy group showed no impairment in emotion or gender recognition ($ps_{\text{Bonferroni}} \geq .485$), exhibiting the same pattern as in Experiment 1.

Discussion

Our single-pulse TMS protocol suggests coexistence of subcortical and cortical pathways in rapid fear processing. Specifically, early disruption of V1/V2 function does not impair fear recognition when visual information is limited. Conversely, when visual accessibility is increased, the same TMS protocol disrupts fear recognition at an early SOA of 30 ms and specializes for LSF filtered fearful information, revealing the conditions under which V1/V2 is involved in rapid fear processing. These results highlight the adaptive recruitment of each pathway based on the visual environment.

To ensure that the TMS effects target prioritized fear processing, we implemented two critical experimental manipulations. First, we applied single-pulse TMS at specific time points after stimulus onset, allowing temporal control over the target brain region at specific stages of visual processing. Since rapid fear processing in the amygdala occurs within 90 ms (Inagaki et al., 2023; Méndez-Bértolo et al., 2016; Sato et al., 2011; Y. Wang, Luo, et al., 2023), only effects observed at the 30- and 60-ms SOAs are indicative of influence on rapid fear processing. Second, as rapid and preconscious processing is typically observed with coarse fear-related information (Méndez-Bértolo et al., 2016; Vuilleumier et al., 2003; Yu et al., 2024; Zhu et al., 2021), the recognition of fear in LSF stimuli serves as a key indicator. Indeed, in Experiment 2, impairment on fear recognition was observed at an early SOA of 30 ms and was specific to LSF information, ruling out the possibility that the observed impairment stemmed from other visual processes.

While the null effects of TMS on LSF fear recognition at the SOAs of 30 and 60 ms in Experiment 1 suggest independence of early visual cortex, this evidence alone is not sufficient to confirm the existence of a subcortical pathway. There remains the possibility that short-cut pathways bypass V1/V2 to transmit fear-related information to the amygdala. However, several factors make this explanation unlikely. First, complementing the findings of Experiment 1, rapid and LSF-specific processing of fear has been consistently linked to subcortical pathways across multiple lines of evidence (Méndez-Bértolo et al., 2016; Morris et al., 1998, 1999; Y. Wang, Luo, et al., 2023).

In contrast, while the cortical pathway model suggests that these findings are explainable by the existence of multiple short-cut pathways, there is no direct evidence supporting fear processing via any specific short-cut pathway. Furthermore, even if such short-cut pathways exist, it is reasonable to assume that the same cortical pathway would be recruited for the same stimuli and task across experiments. Given that Experiment 2 identified V1/V2 as a critical hub for the cortical pathway, fear processing in Experiment 1—if dependent on the cortical pathway—should also rely on V1/V2 function. The observed independence of V1/V2 in Experiment 1 therefore provides strong evidence against the involvement of cortical pathways in rapid fear processing under conditions of limited visual information.

Our findings underscore the adaptive nature of visual pathway recruitment. We theorize that the human brain minimizes the loss of critical information by flexibly engaging the most efficient pathway based on environmental conditions. When visual information is adequate, cortical pathways—capable of rapid emotion processing via short-cut routes—are preferentially recruited, enabling the processing of relevant information. However, under limited visual accessibility, the fearful information is too rapid and weak to engage the cortical pathway or the reentrant cortico-subcortical feedback such that the critical threat-related information is processed by the subcortical pathway, often outside of conscious awareness (Brooks et al., 2012; Diano et al., 2017; Tamietto & de Gelder, 2010). Future research is needed to explore whether dual-pathway applies to other emotions and stimulus types, as well as investigate additional factors to visual accessibility that may drive this flexibility.

In summary, this study provides causal evidence for the coexistence and adaptive recruitment of subcortical and cortical pathways in rapid fear processing. The dual-pathway arrangement may optimize the brain's ability to efficiently process external threats.

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