



The neural mechanism underlying the effects of preceding contexts on current categorization decisions



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ABSTRACT

Preceding contexts strongly influence current decision-making. To elucidate the neural mechanism that underlies this phenomenon, magnetoencephalographic signals were recorded while participants performed a binary categorization task on a sequence of facial expressions. The behavioral data indicated that the categorization of current facial expressions differed between the contexts shaped by the immediately preceding expression. We found that the effects of the preceding context were linked to prestimulus power activities in the low-frequency band. However, these context-dependent neural markers did not reflect behavioral decisions. Rather, the beta power observed primarily after stimulus onset and located at distinct sensors was predictive of the trial-by-trial decisions. Despite these results, the coupling strength between context-dependent and decision-related power differed between preceding contexts, suggesting that the context-dependent power interacted with decision-related power in a systemic manner and in turn biased behavioral decisions. Taken together, these findings suggest that categorization decisions are mediated by a series of power activities that coordinate the influence of preceding contexts on current categorization.

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1. Introduction

Decisions are not made in isolation. Instead, they are often made within a rich context shaped by previous material. Indeed, it has long been established that preceding contexts play a crucial role in biasing current decision-making, as was conceptualized by the adaptation-level theory (Helson, 1964) or the framing effect for example (Tversky and Kahneman, 1981). However, most prior studies have focused on characterizing the flow of neural information in mediating decisions about current percepts, largely ignoring the role of preceding contexts (Freedman et al., 2003; Heekeren et al., 2004; Philiastides and Sajda, 2006). Although a few neuroimaging studies have attempted to determine how prior information is represented in the brain (Gorlin et al., 2012; Preusschhof et al., 2010; Summerfield and Koechlin, 2008), the neural mechanism underlying how a decision is dynamically adjusted according to preceding contexts remains unclear.

To understand the influence of preceding contexts on current decision-making, the present study capitalized on sequential effects during categorization decisions. This trial-to-trial transition effect has been widely investigated in previous behavioral research (Hampton et al., 2005; Stewart et al., 2002; Zotov et al., 2011).

When categorizing a sequence of facial expressions in which the physical features of the stimuli morph continuously between two categories of emotion, a recent study (Hsu and Yang, 2013) has shown that the categorical judgments of the current expression vary according to the local sequential context provided by the immediately preceding expression. For example, there is a decreased categorization accuracy to a morphed fearful expression when it is preceded by a *distant* fearful prototype (large morphing distance to the current stimulus) as opposed to a *nearby* fearful morph (small morphing distance to the current stimulus). However, these sequential effects are limited to two successive stimuli, as the preceding context provided by the expression presented two trials earlier has little impact on the categorization judgment of the current expression. Although the underlying psychological mechanism remains inconclusive, behavioral and modeling studies have suggested that sequential effects involve using relative difference information between successive items to inform categorization decisions (Hampton et al., 2005; Stewart et al., 2002). According to these models, when the interstimulus distance is large (e.g., a distant preceding fearful prototype vs. a current fearful morph), participants tend to categorize the current stimulus as further from the category of the preceding stimulus (fewer “fear” decisions for the current stimulus). This decision bias may result from a shift in internal criteria for the current category representation after viewing a distant preceding stimulus: the criterion-shift account (Treisman and Williams, 1984; Zotov et al.,

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2011). Alternatively, the bias may reflect the use of a similarity/dissimilarity comparison between the preceding and current stimuli as evidence for categorization decisions; in other words, two dissimilar stimuli are perceived as belonging to two distinct categories: the similarity/dissimilarity account (Stewart and Brown, 2005).

In this study, participants performed a similar binary categorization task on a sequence of facial expressions that included continua of morphs ranging from fearful to neutral, while magnetoencephalography (MEG) signals were recorded. This methodology allowed us to capture the temporal dynamics concerning how neural activity at various processing stages coordinates the influence of sequential contexts provided by preceding facial expressions on the categorization of a current facial expression. Previous studies have suggested that spectral analysis of beta- and gamma-band activity and frequency-specific neural connectivity are particularly valuable for providing mechanistic information regarding decision processing (Hipp et al., 2011; Siegel et al., 2011). Therefore, the goals of this study were to identify the power activities underlying the expression-based sequential effects revealed from behavioral performance and subsequently to characterize how these activities ultimately shape categorization decisions.

2. Materials and methods

2.1. Participants

A total of 17 right-handed participants with no neurological or psychiatric history participated in this study (13 males, mean age = 28 years, range = 23–32 years). All participants had normal or corrected-to-normal vision and provided written informed consent prior to their participation.

2.2. Stimuli

Ten continua of morphed facial expressions from fearful to neutral were generated using FantaMorph (Abrosoft). In each continuum, a neutral prototype was morphed 12.5%, 25%, 37.5%, 50%, 62.5%, 75%, and 87.5% of the physical distance to an identity-matched fearful prototype, resulting in 9 face images (Fig. 1A). The

stimuli within each continuum were adjusted and matched according to low-level physical attributes, such as luminance, using the SHINE toolbox (Willenbockel et al., 2010). Prototypical examples of fearful and neutral expressions were selected from the FEEST database (Young et al., 2002). A total of 90 face stimuli were used (10 continua with distinct identities \times 9 stimuli per continuum). The face images subtended a horizontal visual angle of 2.4° and a vertical angle of 2.7° around the center of the screen. The stimulus presentation was controlled using Psychtoolbox (Brainard, 1997).

2.3. Procedure

Each trial began with a fixation cross located at the center of the screen for 600–800 ms, followed by the presentation of a facial expression for 300 ms and then a blank screen for 250 ms. Next, a response window was displayed with two choices, “fearful” and “neutral”, placed on either side of the fixation cross. The positions of these response choices were randomized across trials. Participants had up to 3 s to categorize the face they had just viewed as fearful or neutral by pressing a button with their right index or middle finger. Performance feedback was not provided. The button press initiated a new trial after a 1400–1800 ms inter-trial interval. The participants took part in two sessions on separate days, with 3 repetitions per continuum. In each session, the participants completed 15 blocks, with a break between blocks. The trials were blocked by continuum. Within each block, each face was randomly repeated 9 times, resulting in a total of 81 trials (9 repetitions \times 9 faces per continuum). The participants first completed 1–2 blocks of practice trials to familiarize themselves with the procedure. The practice trials included a separate set of face continua that were not used in the actual experiment.

A central goal of this study was to understand how categorization decisions on current stimuli varied according to the preceding contexts. Because evidence has shown that sequential contexts exert the strongest influence on the categorization of ambiguous stimuli (Hampton et al., 2005; Hsu and Yang, 2013; Stewart et al., 2002; Zotov et al., 2011), all of our analyses focused exclusively on ambiguous expressions at the boundaries between two emotion categories, where the percentages of “fearful” and “neutral” responses were approximately 50%. This analysis strategy may also allow us both to examine how categorization

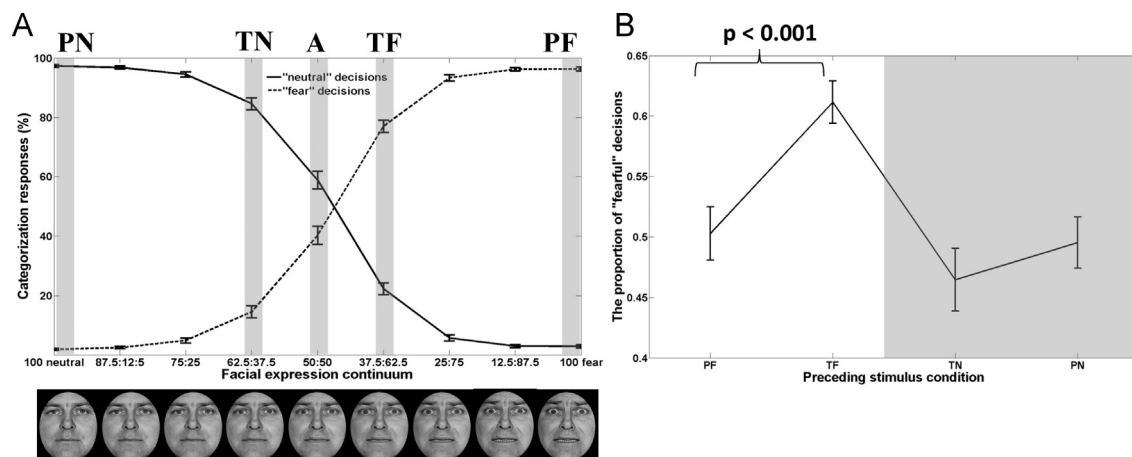


Fig. 1. Behavioral performance. (A) Categorization of facial expressions in one representative continuum. The expression continuum progresses from the fearful prototypes to the neutral prototypes in 8 steps. The notations PF, TF, A, TN and PN represent the fearful prototypes, the fearful morphs that were closest to the ambiguous expressions, the ambiguous expressions, the neutral morphs that were closest to the ambiguous expressions and the neutral prototypes, respectively. Notably, because the category boundary was located between the 62.5:37.5 and 37.5:62.5 fearful:neutral morphs across continua and individuals, the gray bars in the figure simply provide an example of how the expression stimuli were selected to analyze the sequential effects. Error bars represent \pm SEM. (B) The proportion of “fearful” categorization decisions of the current ambiguous expressions as a function of the four preceding expression types. The shaded region indicates that the preceding stimuli are from the “neutral” category. Error bars represent \pm SEM.

decisions alternated in the face of identical visual stimulation from ambiguous expressions and to obtain an approximately equal number of “fearful” and “neutral” decision trials to identify decision-related correlates (see ROC analysis).

2.4. MEG recording

MEG recordings were performed using a whole-head system comprising 160-axial-gradiometer channels (Yokogawa, Co., Tokyo). The data were digitized at 1000 Hz. To minimize head movements between blocks and across sessions, the head positions of the participants relative to the MEG sensors were monitored using a set of head localization coils placed at the nasion and at the left and right ear canals. FieldTrip (Oostenveld et al., 2011) and MATLAB (MathWorks, Natick, MA) software were used for data preprocessing, analysis and visualization.

2.5. Spectral analysis

The continuous data were first segmented into 1800-ms epochs starting from 800 ms before the onset of the facial expression stimulus. Any trials that contained eye movements, eye blinks, and muscular artifacts were rejected after visual inspection and semi-automatic functions implemented in Fieldtrip. For every sensor-frequency (8–100 Hz)-time point (−350 to 550 ms after facial expression onset) in each trial, the data were subjected to spectral analysis to estimate the signal power using Morlet wavelets with the ratio of the central frequency to the bandwidth fixed at 7 (Tallon-Baudry et al., 1996). This signal power was then averaged across trials in each experimental condition for each participant. To compensate for the $1/f$ decay, the averaged power activity was then normalized to a baseline from 350 to 150 ms preceding the onset of the face stimulus. This standard normalization procedure involved a logarithmic base-ten transformation of the power activity at each sensor-time-frequency point relative to the mean power throughout the baseline period at the corresponding sensor and frequency. By definition, the units for the normalization were decibels (db).

To analyze the spectral power at the single-trial level (for power connectivity and ROC analyses), single-trial Z-normalization was performed using the following equation (Grandchamp and Delorme, 2011):

$$P^z(s, f, t, n) = \frac{P(s, f, t, n) - \bar{P}(s, f, n)}{\sigma(s, f, n)}$$

In this formula, P^z denotes the Z-normalized power activity for each sensor s , frequency f , time t , and trial n ; P denotes the original single-trial activity; and \bar{P} and σ denote the mean power and the standard deviation, respectively, for all time points throughout the epoch (−350 to 550 ms). The full-trial epoch was used here because this procedure was less sensitive to noise compared with the classical approach using the pre-stimulus baseline (Grandchamp and Delorme, 2011).

2.6. Cluster-based Randomization test

To determine whether the data between experimental conditions were significantly different, cluster-based permutation tests were conducted (Maris and Oostenveld, 2007). This statistical test does not require specific assumptions regarding the shape of the population distribution and allows multiple comparison problems to be controlled (Maris and Oostenveld, 2007). For these tests, the data (e.g., power activity) between experimental conditions were quantified by means of paired t -tests for every sensor-time (−350 to 550 ms) -frequency sample (8–100 Hz). Those samples with t

values exceeding the threshold ($p < 0.05$) were then clustered into connected sets based on spatial, temporal or frequency adjacency with a minimum of two contiguous sensors. The cluster with the maximum sum of t values was used as a test statistic. A distribution of test statistics was then generated by randomly permuting the data across the conditions within each participant and recalculating the test statistic 1000 times using a Monte Carlo estimate (Manly, 1997). Lastly, the p Values were determined by evaluating the proportion of the obtained distribution that resulted in a test statistic larger than the observed statistic.

2.7. Receiver operating characteristic (ROC) analysis

To identify decision-related neural correlates of the ambiguous expressions, ROC analysis was performed (Green and Swets, 1966) to quantify the link between trial-by-trial behavioral decisions and associated power activities. The trials in which the stimuli were ambiguous expressions were first sorted according to the decision outcome. There were approximately an equal number of “fearful” and “neutral” decision trials for the ambiguous expressions (“fearful” trials: mean \pm SEM = $100 \pm 5\%$; “neutral” trials: $93 \pm 4\%$; paired t -test on the number of trials, $t(16) = 1.49$, $p = 0.16$). Next, the distribution of power activities in the “fearful” and “neutral” trials could be determined for each sensor-time-frequency sample. These two distributions may be regarded as the signal and noise distributions in signal detection theory. For every sample, an ROC curve was constructed by varying the criterion between the minimum and maximum values of both distributions. Therefore, each point on the ROC curve represents the proportion of power activities in the “fearful” trials that exceeded a given criterion compared with the proportion of power activities in the “neutral” trials that exceeded the same criterion. For each sample, the area under the ROC curve (AUC) was computed and transformed into A' , where $A' = 2AUC - 1$. The A' index represents how well a sensor-time-frequency sample was able to predict the decision outcomes of ambiguous expressions based on single-trial power activities. Both positive and negative A' values indicate that the power activities of a given sample could differentiate subsequent fearful-neutral decisions at a probability better than chance. Specifically, for the samples in which the A' values were negative, “fearful” decisions were associated with lower power, and “neutral” decisions were associated with higher power. For the samples in which the A' values were positive, the reverse was true.

2.8. Power connectivity

A power correlation was performed to estimate coupling between context-dependent and decision-related power activities across multiple trials (Cohen, 2014). For this analysis, the power activities in the sensor-time-frequency window during which the activities reflected the influence of preceding contexts (i.e., the context-dependent window, see Results Section 3.2 for more details) and the power activities in the sensor-time-frequency window during which the activities reflected behavioral categorization reports (i.e., the decision-related window, see Results Section 3.3 for more details) were extracted and averaged across all samples. After the obtained data were rank-transformed, the Spearman correlation coefficient “ ρ ” was calculated because the power data were not normally distributed:

$$\rho = \frac{\sum_{n=1}^N (P_n^c - \bar{P}^c) \times (P_n^d - \bar{P}^d)}{\sqrt{\sum_{n=1}^N (P_n^c - \bar{P}^c)^2 \times \sum_{n=1}^N (P_n^d - \bar{P}^d)^2}}$$

In this formula, P_n^c represents the averaged power in the context-dependent window in trial n and \bar{P}^c represents the mean of P_n^c

across all trials. P_n^d represents the averaged power in the *decision-related* window in trial n , and P^d represents the mean of P_n^d across all trials. Finally, N represents the total number of trials in a given experimental condition. Before any statistical evaluation was performed, the obtained correlation coefficients were Fisher's Z -transformed because the correlation coefficients exhibited a bounded distribution between -1 and $+1$ and were therefore not drawn from a normal distribution:

$$\rho^z = 0.5 \times \ln\left(\frac{1 + \rho}{1 - \rho}\right)$$

In this formula, ρ^z denotes the Z -transformed Spearman coefficient.

3. Results

3.1. Behavioral performance

For each expression continuum, categorization data were calculated as the proportion of choices corresponding to the “fearful” or “neutral” category for each morphed face. The responses to stimuli at the same morph steps were first averaged, irrespective of their preceding contexts. Fig. 1A shows the data from one representative continuum collapsed across all individuals. Notably, the exact location of the category boundaries, where categorization performance was near 50%, lay between the 67.5:37.5 and 37.5:62.5 fearful:neutral morphs across the continua and across the participants. Despite this inconsistency, a highly consistent picture still emerged for each continuum. As previously described (Calder et al., 1996), the data clearly indicated the categorical perception of facial expressions. More specifically, every continuum contained two separate regions with an abrupt shift, and each region belonged to the emotional category that corresponded to the prototypical expressions at that end of the continuum. We also checked whether the pattern of categorical perception might differ across the experiment due to face familiarity effects (Angeli et al., 2008; Beale and Keil, 1995). Because each continuum was repeated three times in separate blocks, the categorization data along each continuum were calculated separately in the first and the third block and then pooled across the continua. The results did not reveal any significant difference in the categorization data of identity continua between blocks (two-way repeated measures ANOVA, interaction between the factors of time block and morph level: $F(8, 128) = 0.79$, $p = 0.61$), indicating that face familiarity did not significantly affect the categorical perception of facial expression.

To control for variability in the locations of the category boundaries to enable a proper examination of whether sequential effects were present, we analyzed whether the categorization responses to ambiguous expressions at the category boundaries differed according to the preceding context because this region is where the strongest sequential effects have previously been observed (Hampton et al., 2005; Hsu and Yang, 2013; Stewart et al., 2002; Zotov et al., 2011). Accordingly, the categorization responses to the ambiguous expressions (A in Fig. 1A, mean percentage of “fearful” decisions \pm SEM: $51.68 \pm 1.18\%$, collapsed across continua and participants; mean number of trials \pm SEM: 237 ± 4) were sorted based on whether the ambiguous expressions were preceded by one of the following *highly recognizable* preceding expressions: prototypical fearful expressions (PF in Fig. 1A, $97.29 \pm 0.30\%$; 49 ± 2 trials), fearful morphs that were closest to the ambiguous expressions (TF in Fig. 1A, $92.38 \pm 0.55\%$; 48 ± 2 trials), prototypical neutral expressions (PN in Fig. 1A, mean proportion of “neutral” decisions \pm SEM: $97.69 \pm 0.48\%$; 53 ± 2 trials),

or neutral morphs that were closest to the ambiguous expressions (TN in Fig. 1A, $92.88 \pm 0.39\%$; 61 ± 2 trials). The gray bars in Fig. 1A illustrate how the ambiguous expressions and the four types of preceding stimuli were selected.

The proportions of current ambiguous expressions labeled as “fearful” varied significantly as a function of the four preceding stimulus conditions (one-way repeated measures ANOVA, $F(3, 48) = 9.63$, $p < 0.001$; Fig. 1B). To further understand whether the emotional categories of the preceding stimuli and the relative distance between the preceding and current stimuli played a role in this sequential effect, the data were examined separately for the trials in which the preceding stimuli were from the fearful (white zone) or neutral (gray zone) category. When the preceding stimuli were fearful, the participants were more likely to categorize the current ambiguous expressions as “fearful” after viewing the nearby TFs compared with the distant PFs (paired t -test, $t(16) = 3.71$, $p = 0.002$). In contrast, the preceding contexts shaped by the neutral expressions at different distances (i.e., PNs and TNs) did not differentially bias participants’ judgment of the current ambiguous expressions ($t(16) = 1.05$, $p = 0.311$). Thus, expression-based sequential effects, in which the categorization of current ambiguous expressions differed between the preceding TF and PF conditions, were demonstrated.

It should be emphasized that we did not perform comparisons between preceding stimuli from different emotion categories for the following reasons. First, emotional effects might confound the sequential effects. In addition, because of variability in the category boundaries, the relative distance between the preceding PF and the ambiguous expression and the distance between the preceding PN and the ambiguous expression, for instance, may have also differed depending on continua and individuals. Therefore, it would have been difficult to control and subsequently examine the role of relative distance in the comparisons.

3.2. Context-dependent neural correlates

To characterize the neural activity underlying the observed sequential effects, a wavelet transform was applied to the MEG signals, and time–frequency representations of the power spectrogram of the current ambiguous expression trials were computed for each sensor. Guided by the behavioral data, cluster-based permutation tests were conducted to identify the context-dependent neural correlates that fulfilled the following criteria. First, differential power activities should be observed in the neural correlates if the ambiguous expressions are preceded by a PF relative to a TF. Second, within the same correlate, no significant power difference should be observed between the preceding PN and TN conditions. It is important to note that at the initial stage of this analysis, it was unclear whether context-dependent correlates could ultimately determine behavioral decisions. Therefore, we did not adopt a more stringent criterion to link context-dependent correlate activity to decision outcomes.

Based on our criteria, we identified a neural correlate that represented the effect of the preceding contexts (Fig. 2A). When ambiguous expressions were preceded by a PF, the power activity over the right anterior sensors was significantly reduced prior to stimulus onset in the low-frequency range (10–30 Hz, -120 to 80 ms; cluster-based permutation test, $p = 0.02$). The power activities between the preceding PN and TN conditions were also compared (Fig. 2B). However, no significant power difference was observed in any sensor-time-frequency sample ($p = 0.10$), even when the analysis was restricted to the aforementioned context-dependent window ($p = 0.46$). These results can be summarized in Fig. 2C as the mean power activity in the context-dependent window for each preceding stimulus condition. In summary, corresponding to the behavioral data, different types of preceding

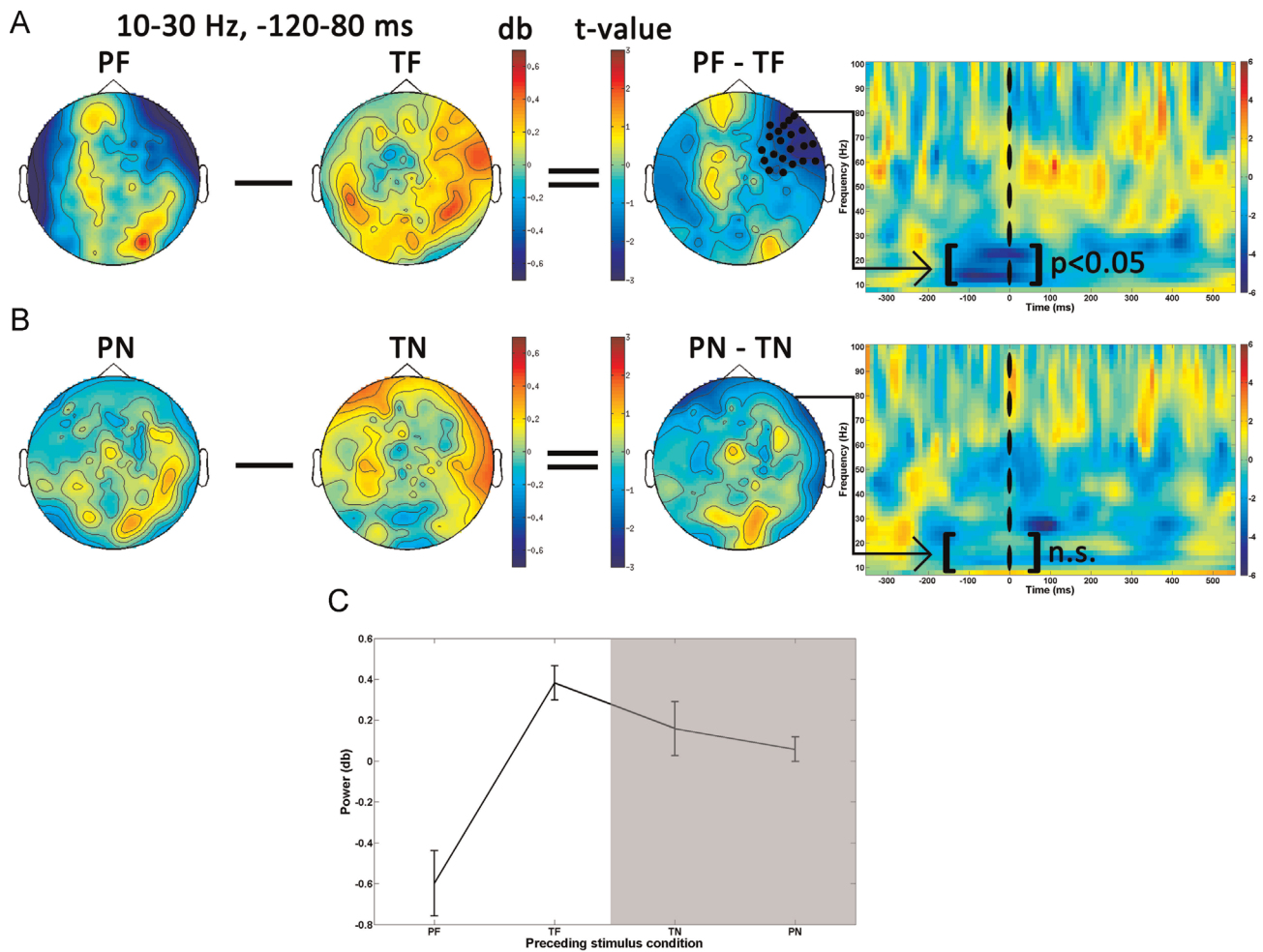


Fig. 2. Context-dependent neural correlates. (A) The power activities in the preceding PF and TF conditions (left panel) and the differences between the two conditions (right panel). In the scalp topography on the right panel, the black dots represent the clusters of sensors that showed significant power differences. The far right panel is the time–frequency representation of spectral power for the MEG sensor AG99. The dotted line indicates the onset of facial expression stimuli, and the black brackets represent the windows during which power activities between the preceding PF and TF conditions were significantly different. (B) The power activities in the preceding PN and TN conditions (left panel) and the differences between the two conditions (right panel). The conventions are the same as in (A). (C) The context-dependent power activities as a function of the preceding stimulus conditions. The data were obtained by collapsing the power activities from the highlighted sensors between 10 and 30 Hz and between –120 and 80 ms in each condition. The shaded region indicates that the preceding stimuli are from the “neutral” category. Error bars represent \pm SEM.

contexts provided by fearful expressions, but not neutral expressions, had differential impacts on the low-frequency power, and this impact began as early as 120 ms before stimulus onset.

3.3. Decision-related neural correlates

We next tested whether the *context-dependent* power could reflect behavioral categorization decisions. To accomplish this goal, the ambiguous expression trials were sorted according to “fearful” or “neutral” behavioral reports, regardless of the four preceding stimulus conditions. For each group of trials, the power activities in the previously identified context-dependent window were extracted and then averaged. No significant difference was observed between the averaged power activities in the ‘fearful’ and ‘neutral’ trials (paired t -test, $t(16)=1.06$, $p=0.30$), indicating that the *context-dependent* power cannot predict decision outcomes.

To better identify the *decision-related* neural correlates, ROC analysis was performed to quantify the link between *trial-by-trial* behavioral decisions and associated power activities. For each sensor-time-frequency sample, an ROC curve was constructed, and the area under the ROC curve was designated as the A' index (see the Section 2 for more details). This index was used to identify any sensor-time-frequency sample that could predict behavioral

decisions at a probability better than chance (i.e., an A' index $\neq 0$) based on single-trial power activities. Next, cluster-based permutation tests were applied to locate connected sets of samples in which the A' values were significantly higher or lower than zero. A cluster of negative A' values was identified over the left sensor sites between 14 and 32 Hz over the –40 to 120 ms interval ($p < 0.001$; Fig. 3A), indicating that the power activities in the decision-related window were able to differentiate whether a trial was associated with “fearful” or “neutral” decisions at a probability better than chance. To provide a clearer picture of this finding, the ambiguous expression trials were again grouped according to the behavioral decision. The power activities in the *decision-related* window were then averaged for the “fear” and “neutral” decision trials. As shown in Fig. 3B, the negative A' values clearly represent the result that in the decision-related window, “neutral” decisions were associated with higher power activities, whereas “fearful” decisions were associated with lower power activities.

3.3.1. The relationship between context-dependent and decision-related neural activities

To determine the link between context-dependent and decision-related power activities, we first examined whether decision-related power also varied as a function of the preceding contexts.

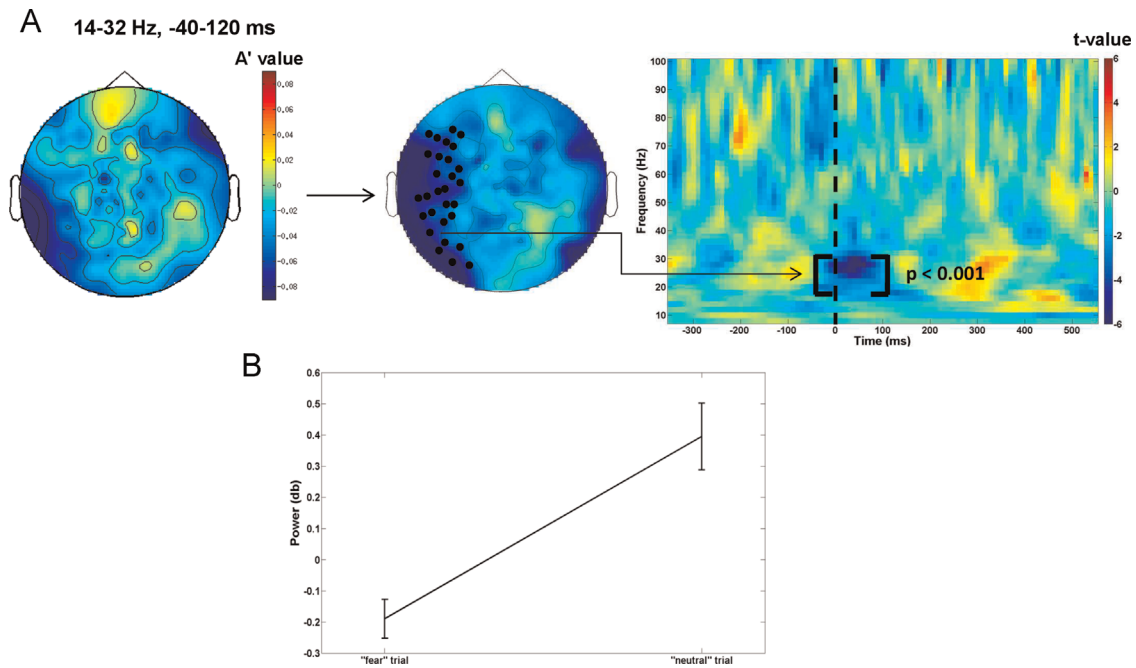


Fig. 3. Decision-related neural correlates. (A) Decision-related activities expressed as the A' indexes and the t statistic values of the A' indexes against zero. The left panel is the scalp topography of the A' indexes. The middle panel is the scalp topography showing the clusters of sensors (black dots) in which the A' indexes were significantly negative. The right panel is the time–frequency representation of the MEG sensor AG50. The dotted line indicates the onset of facial expression stimuli, and the black brackets represent the windows during which the A' indexes were significantly negative. (B) The power activities in the decision-related correlate for “fearful” and “neutral” decision trials. The data were obtained by collapsing the power activities in the highlighted sensors between 14 and 32 Hz and between –40 and 120 ms. Error bars represent \pm SEM.

The ambiguous expression trials were sorted according to the preceding stimulus condition, and the power activities in the *decision-related* window were extracted and averaged for each condition (Fig. 4A). We found that the average power activities in the preceding PF condition were significantly lower than those in the preceding TF condition (paired *t*-test, $t(16)=2.71$, $p=0.002$), but the power activities were comparable between the preceding PN and TN conditions ($t(16)=1.01$, $p=0.33$). Given that a consistent difference between the preceding contexts (PF and TF) was observed in both context-dependent (Fig. 2) and decision-related power (Fig. 4A), we hypothesized that decision-related power might interact with context-dependent power in a systematic manner.

To investigate this potential power-based connectivity, we determined whether the *trial-by-trial* coupling between the context-dependent and decision-related power activities varied according to the preceding context. For this analysis, the power activities were first averaged in a context-dependent or decision-related window for each trial in each preceding stimulus condition. Next,

we computed a Fisher's Z-transformed Spearman correlation coefficient between the averaged context-dependent and decision-related power activities across trials (see the Section 2 for details). We found that the context-dependent power was more strongly correlated with the decision-related power in the preceding TF compared with the preceding PF condition (paired *t*-test on the coefficients, $t(16)=2.41$, $p=0.03$; Fig. 4B). In comparison, no significant difference was found in the power correlation between the preceding TN and PN conditions ($t(16)=0.26$, $p=0.80$). Collectively, the pattern of power correlation across the preceding stimulus conditions strongly agreed with the sequential effects that had been observed in the behavioral analysis, indicating a systematic interaction between the two activities.

3.4. Control analysis

Could the observed sequential effects be attributed to well-established phenomena, such as expression aftereffects or emotional priming effects, given that both effects also involve a biased

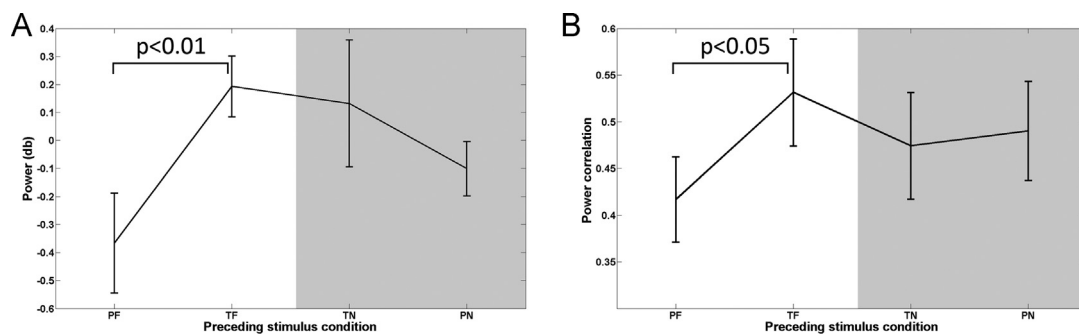


Fig. 4. (A) Decision-related power as a function of the preceding stimulus conditions. The shaded region indicates that the preceding stimuli are from the “neutral” category. Error bars represent \pm SEM. (B) A power correlation between the context-dependent and decision-related power activities as a function of the preceding stimulus types. The power correlation is expressed as a Fisher's Z-transformed Spearman correlation coefficient. The shaded region indicates that the preceding stimuli are from the “neutral” category. Error bars represent \pm SEM.

recognition of a current expression after viewing a preceding expression? In contrast to the experimental procedure adopted in this study, a prolonged presentation of the preceding expression (exceeding one second) is usually required to generate robust aftereffects (Hsu and Young, 2004; Strobach and Carbon, 2013). Moreover, during the adaptation times, participants were required to attentively inspect the preceding stimuli without performing any cognitive task. Emotional priming effects are also unlikely to be the major source of the sequential effects. If the present results are due to emotional priming effects, improved categorization accuracy would have been observed following the presentation of prototypical emotional stimuli compared with prototypical neutral stimuli (Carroll and Young, 2005). However, we failed to observe this pattern in the present results, as there was no significant difference in categorization between the preceding PF and PN (paired *t*-test, $t(16)=0.23$, $p=0.82$) conditions.

Because in the time–frequency analyses, a potential bias might arise from the differing number of trials in each preceding stimulus condition (one-way repeated measures ANOVA, $F(3, 48)=10.32$, $p<0.001$), we repeated the spectral power and power connectivity analyses by randomly selecting an equal number of trials (with a minimum of 30 trials) for each preceding condition. Nevertheless, our findings remained unchanged (all *p* values <0.05).

To determine whether the reported findings were specific, we performed a separate set of analyses using the PNs (i.e., the neutral prototypes) as the controls. In other words, we checked whether the aforementioned context-dependent, decision-related and power connectivity neural effects could also be found in the time–frequency data from the PN trials under similar experimental conditions. The PN face stimuli were chosen because the behavioral responses to the PNs were not significantly different (paired *t*-test, $t(16)=0.01$, $p=0.87$) when they were preceded by the PFs (mean proportion of “neutral” decisions about PNs \pm SEM: $96.96 \pm 0.01\%$) compared with when preceded by the TFs ($97.07 \pm 0.01\%$), indicating the absence of a sequential effect in the PN trials. Here, the preceding stimulus conditions, the PFs and TFs, were defined in the same manner as before, in which the PFs denote the prototypical fearful expressions and the TFs denote the fearful morphs that were closest to the ambiguous expressions. Given that the behavioral responses to the current PNs did not significantly differ between the preceding PF and TF conditions, we expected that our MEG findings could not be replicated. To test this hypothesis, we first examined the presence of context-dependent power by extracting the mean power from the previously defined context-dependent window separately in the preceding PF and TF conditions for the PN trials. As expected, the mean power activities were not significantly different between these two conditions ($t(16)=1.51$, $p=0.15$). Because the majority of the PN trials were categorized as “neutral” ($98.14 \pm 0.00\%$), it is difficult to evaluate whether the power activities in the previously defined decision-related window could predict behavioral decisions. Nevertheless, we were still able to calculate the power correlations between the mean power activities in the context-dependent and decision-related windows for the PNs. No significant difference in power correlation was observed between the preceding PF and TF conditions ($t(16)=1.28$, $p=0.22$), confirming that our reported findings did not indicate a generic phenomenon.

The present study recorded MEG data during two separate sessions to ensure a sufficient number of trials for analysis. Would the data from the first and the second sessions be qualitatively or quantitatively different and therefore affect our findings? To address this concern, the power activities (all sensors, 8–100 Hz, –350 to 550 ms) of the ambiguous expressions trials in each session were separately computed, regardless of the preceding stimulus condition. No significant difference was found between

sessions in any sensor–time–frequency point (cluster-based permutation test, $p=0.89$). The same effects were also obtained when the analyses were restricted to the previously defined context-dependent and decision-related windows (all *p* values >0.79) and when the power activities were separately calculated for each preceding stimulus condition (all *p* values >0.3). However, it should be emphasized that in the latter case, some of the data points were based on as few as 14 trials. In addition, if the reported findings are due to the distinct nature of the data from different sessions, these findings should also be observed using the PN trials instead of the ambiguous expression trials. This view obviously does not agree with the results of the above control analysis.

4. Discussion

By capitalizing on sequential effects, this study provides novel evidence that current categorization depends on the contexts shaped by immediately preceding stimuli and that this phenomenon is mediated by a series of power activities on different sensor, time and frequency scales. Prior to stimulus onset, differing preceding contexts differentially affected low-frequency power activities over the right anterior sensors. However, the context-dependent neural markers were not able to determine behavioral outcomes. Instead, beta-band power, located on the left sensors and observed primarily after context-dependent power, could predict trial-by-trial decisions. Despite this finding, the coupling strength between context-dependent and decision-related power differed between preceding contexts, suggesting that context-dependent power may still be able to exert its influence on categorization decisions by modulating the decision-related power.

4.1. Sequential effects in behavioral categorization

Our behavioral results are consistent with prior studies, demonstrating that the relative difference information between preceding and current stimuli could provide a basis for categorization (Hampton et al., 2005; Hsu and Yang, 2013; Stewart et al., 2002; Zotov et al., 2011). When the relative distance between the two successive facial expressions was increasingly large (PFs vs. ambiguous expressions), category representation of the current stimulus might be shifted away following the distant preceding stimulus (Treisman and Williams, 1984; Zotov et al., 2011), or participants might believe that the two stimuli were dissimilar (Stewart and Brown, 2005). As a result, the current stimulus was judged as away from the category of the preceding stimulus, yielding fewer “fearful” decisions on ambiguous expressions when they were preceded by the distant PFs relative to the nearby TFs. Prior literature (Calder et al., 2000) has shown that the emotional intensity and morphing distance are intrinsically entwined. For example, a larger morphing distance away from the fearful prototype but toward the neutral prototype is accompanied by a lower intensity rating for fear. We therefore suggest that relative information between the preceding and current stimuli may represent differences in both the perceptual and emotional attributes of the stimuli.

Intriguingly, no sequential effect was observed between the preceding PN and TN conditions, which might reflect the nature of the neutral expression stimuli employed in this study. For the participant, the psychological distance between the PNs and the ambiguous expressions and the distance between the TNs and the ambiguous expressions might be similar, even though the physical distances of the facial features in these two pairs are different, thereby eliminating any sequential effects.

4.2. The effects of preceding contexts on prestimulus, low-frequency power

This study reveals that the preceding contexts (the PF and TF conditions) were able to differentially influence low-frequency power as early as 120 ms before stimulus onset. Previous studies have shown that prestimulus, low-frequency power plays a role in regulating subsequent behavioral performance (Babiloni et al., 2006; van Dijk et al., 2008; Linkenkaer-Hansen et al., 2004). However, in the present study, context-dependent power was not directly involved in forming behavioral decisions, as indicated by the observation that the mean power in the context-dependent window was not able to differentiate “fearful” from “neutral” decisions, and the decision-related correlates identified by the ROC analysis were observed in separate time intervals and sensor locations.

What is the functional role of context-dependent power? Although the power activities occurred long before the face stimuli were presented, it is unlikely that those activities index a preparation process in which the fixation cross acts as a prime to prepare the participants for the upcoming stimuli. For example, this interpretation cannot explain why the pre-stimulus power differed between the PF and TF conditions, given that the same pre-stimulus fixation cross, with no specific cueing effect, was used in all preceding stimulus conditions. Alternatively, a more plausible interpretation is that pre-stimulus power reflects the influence of previous contexts in the trial sequence. Previous research has suggested that low-frequency power, particularly in the beta-band range, is related to maintaining past cognitive information (Engel and Fries, 2010; Siegel et al., 2011). Accordingly, the observed context-dependent power activities might signal the mechanism by which cognitive information from previous trials is carried over to current trials. Furthermore, within the framework of a criterion-shift account on sequential effects (Treisman and Williams, 1984; Zotov et al., 2011), we also suggest that this carry-over information from preceding trials may modulate participants' internal criteria for category representations and thereby bias current categorization decisions. As introduced previously, two major models have been proposed to account for sequential effects during categorization: the criterion-shift and similarity–dissimilarity accounts. Here, we favor the criterion-shift account because the characteristics of context-dependent power are more compatible with a criterion-shift rather than a similarity/dissimilarity account. The similarity/dissimilarity model contends that sequential effects reflect the computation of similarity/dissimilarity between preceding and current stimuli as evidence to inform perceptual decisions. This proposition obviously contradicts the observation that context-dependent power was observed before face stimulus onset. However, the involvement of similarity/dissimilarity computation cannot be completely ruled out because context-dependent power persisted even after stimulus onset, and it is also possible that this computation may operate at a processing stage during a later time period, such as the decisional stage. Future empirical and computational testing is required to determine the precise nature of context-dependent power and its relation to the existing psychological models of sequential effects.

4.3. Decision-related beta power during categorization decisions

This study indicates that beta power, located at a distinct sensor-time window relative to context-dependent power, could determine behavioral decisions. The involvement of beta power in decision-making has been previously reported in studies of both monkeys (Buschman et al., 2012) and humans (Donner et al., 2009, 2007). Because beta power is commonly engaged during sensorimotor functions (Crone et al., 1998; Pfurtscheller et al., 2003;

Pfurtscheller and Lopes da Silva, 1999), previous research has suggested that decision-related beta power observed before movement execution reflects motor anticipation (Donner et al., 2009). Consistent with this idea, we also observed an early occurrence of decision-related beta power activities before the button press. In addition, this activity was spread over the sensorimotor region and was most prominent on the left side, which is contralateral to the response movement that the participants made with their right fingers. Thus, the observed decision-related beta power activities likely reflect intrinsic rhythms induced by sensorimotor cortical activation.

4.4. The role of power connectivity between context-dependent and decision-related neural correlates

Power-based connectivity has been previously linked to interactions between different processing stages (Furl et al., 2014; de Lange et al., 2008). For example, research on sensorimotor decision-making has suggested that coupling between power activity during the sensory stage of processing (area MT) and power activity during the motor stage of processing (area M1) represents the integration of sensory evidence into motor plans for making decisions (Donner et al., 2009). By correlating the context-dependent and decision-related power activities, our results demonstrate that the strength of power coupling between the two differs as a function of the preceding contexts. Moreover, variations in the coupling strength closely followed the pattern of sequential effects revealed during behavioral performance. Taken together, these data suggest that the effects of preceding contexts, as mediated by the context-dependent power, may interact with decision-related power via power connectivity. These interactions might ultimately affect decision-related power and in turn bias behavioral decisions.

Notably, the effect of field spread severely limits the interpretation of the connectivity analysis results (Schoffelen and Gross, 2009) because they might merely reflect volume conduction of the same activity rather than connectivity between different activities. Nevertheless, our findings are built upon an analysis of the condition differences in power correlations, which were calculated based on power activities at different time lags across separate frequency ranges. Thus, we suggest that these data could be reasonably construed as reflecting genuine connectivity (Cohen, 2014).

5. Conclusion

This study highlights how the human brain utilizes power activities at different sensor-time-frequency scales to coordinate the interaction between preceding contexts and current categorization decisions. We suggest that the prestimulus power in the low-frequency band may provide a window to tap into the effects of preceding contexts. Furthermore, the power connectivity between the context-dependent prestimulus power and decision-related correlates may shed light on the mechanism underlying how preceding contexts affect current decision-making processes.

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References

- Angeli, A., Davidoff, J., Valentine, T., 2008. Face familiarity, distinctiveness, and categorical perception. *Q. J. Exp. Psychol.* 61, 690–707.
- Babiloni, C., Vecchio, F., Bultrini, A., Luca Romani, G., Rossini, P.M., 2006. Pre- and poststimulus alpha rhythms are related to conscious visual perception: a high-resolution EEG study. *Cereb. Cortex* 16, 1690–1700.
- Beale, J.M., Keil, F.C., 1995. Categorical effects in the perception of faces. *Cognition* 57, 217–239.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10, 433–436.
- Buschman, T.J., Denovellis, E.L., Diogo, C., Bullock, D., Miller, E.K., 2012. Synchronous oscillatory neural ensembles for rules in the prefrontal cortex. *Neuron* 76, 838–846.
- Calder, A.J., Rowland, D., Young, A.W., Nimmo-Smith, I., Keane, J., Perrett, D.I., 2000. Caricaturing facial expressions. *Cognition* 76, 105–146.
- Calder, A.J., Young, A.W., Perrett, D.I., Etcoff, N.L., Rowland, D., 1996. Categorical perception of morphed facial expressions. *Vis. Cogn.* 3, 81–117.
- Carroll, N.C., Young, A.W., 2005. Priming of emotion recognition. *Q. J. Exp. Psychol. A: Hum. Exp. Psychol.* 58, 1173–1197.
- Cohen, M.X., 2014. *Analyzing Neural Time Series Data: Theory and Practice*. MIT Press, Cambridge MA.
- Crone, N.E., Miglioretti, D.L., Gordon, B., Lesser, R.P., 1998. Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. II. Event-related synchronization in the gamma band. *Brain* 121, 2301–2315.
- de Lange, F.P., Jensen, O., Bauer, M., Toni, I., 2008. Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Front. Hum. Neurosci.* 2, 7.
- Donner, T.H., Siegel, M., Fries, P., Engel, A.K., 2009. Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Curr. Biol.* 19, 1581–1585.
- Donner, T.H., Siegel, M., Oostenveld, R., Fries, P., Bauer, M., Engel, A.K., 2007. Population activity in the human dorsal pathway predicts the accuracy of visual motion detection. *J. Neurophysiol.* 98, 345–359.
- Engel, A.K., Fries, P., 2010. Beta-band oscillations – signalling the status quo? *Curr. Opin. Neurobiol.* 20, 156–165.
- Freedman, D.J., Riesenhuber, M., Poggio, T., Miller, E.K., 2003. A comparison of primate prefrontal and inferior temporal cortices during visual categorization. *J. Neurosci.* 23, 5235–5246.
- Furl, N., Coppola, R., Averbeck, B.B., Weinberger, D.R., 2014. Cross-frequency power coupling between hierarchically organized face-selective areas. *Cereb. Cortex* 24, 2409–2420.
- Gorlin, S., Meng, M., Sharma, J., Sugihara, H., Sur, M., Sinha, P., 2012. Imaging prior information in the brain. *Proc. Natl. Acad. Sci. USA* 109, 7935–7940.
- Grandchamp, R., Delorme, A., 2011. Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Front. Psychol.* 2, 1–14. <http://dx.doi.org/10.3389/fpsyg.2011.00236>.
- Green, D.M., Swets, J.A., 1966. *Signal Detection Theory and Psychophysics*. Wiley, New York.
- Hampton, J.A., Estes, Z., Simmons, C.L., 2005. Comparison and contrast in perceptual categorization. *J. Exp. Psychol.: Learn. Mem. Cogn.* 31, 1459–1476.
- Heekeren, H.R., Marrett, S., Bandettini, P.A., Ungerleider, L.G., 2004. A general mechanism for perceptual decision-making in the human brain. *Nature* 431, 859–862.
- Helson, H., 1964. Current trends and issues in adaptation-level theory. *Am. Psychol.* 19, 26–38.
- Hipp, J.F., Engel, A.K., Siegel, M., 2011. Oscillatory synchronization in large-scale cortical networks predicts perception. *Neuron* 69, 387–396.
- Hsu, S.M., Yang, L.X., 2013. Sequential effects in facial expression categorization. *Emotion* 13, 573–586.
- Hsu, S.-M., Young, A.W., 2004. Adaptation effects in facial expression recognition. *Vis. Cogn.* 11, 871–899.
- Linkenkaer-Hansen, K., Nikulin, V.V., Palva, S., Ilmoniemi, R.J., Palva, J.M., 2004. Prestimulus oscillations enhance psychophysical performance in humans. *J. Neurosci.* 24, 10186–10190.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd ed. Chapman and Hall, London.
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164, 177–190.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011, 156869. <http://dx.doi.org/10.1155/2011/156869> (9 pp.).
- Pfurtscheller, G., Graftmann, B., Huggins, J.E., Levine, S.P., Schuh, L.A., 2003. Spatio-temporal patterns of beta desynchronization and gamma synchronization in corticographic data during self-paced movement. *Clin. Neurophysiol.* 114, 1226–1236.
- Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857.
- Philastides, M.G., Sajda, P., 2006. Temporal characterization of the neural correlates of perceptual decision making in the human brain. *Cereb. Cortex* 16, 509–518.
- Preuschhof, C., Schubert, T., Villringer, A., Heekeren, H.R., 2010. Prior information biases stimulus representations during vibrotactile decision making. *J. Cogn. Neurosci.* 22, 875–887.
- Schoffelen, J.M., Gross, J., 2009. Source connectivity analysis with MEG and EEG. *Hum. Brain Mapp.* 30, 1857–1865.
- Siegel, M., Engel, A.K., Donner, T.H., 2011. Cortical network dynamics of perceptual decision-making in the human brain. *Front. Hum. Neurosci.* 5, 1–12.
- Stewart, N., Brown, G.D.A., 2005. Similarity and dissimilarity as evidence in perceptual categorization. *J. Math. Psychol.* 49, 403–409.
- Stewart, N., Brown, G.D.A., Chater, N., 2002. Sequential effects in categorization of simple perceptual stimuli. *J. Exp. Psychol.: Learn. Mem. Cogn.* 28, 3–11.
- Strobach, T., Carbon, C.C., 2013. Face adaptation effects: reviewing the impact of adapting information, time, and transfer. *Front. Psychol.* 4, 1–12. <http://dx.doi.org/10.3389/fpsyg.2013.00318>.
- Summerfield, C., Koehlin, E., 2008. A neural representation of prior information during perceptual inference. *Neuron* 59, 336–347.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., Pernier, J., 1996. Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J. Neurosci.* 16, 4240–4249.
- Treisman, M., Williams, T.C., 1984. A theory of criterion setting with an application to sequential dependencies. *Psychol. Rev.* 91, 68–111.
- Tversky, A., Kahneman, D., 1981. The framing of decisions and the psychology of choice. *Science* 211, 453–458.
- van Dijk, H., Schoffelen, J.M., Oostenveld, R., Jensen, O., 2008. Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J. Neurosci.* 28, 1816–1823.
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G.O., Gosselin, F., Tanaka, J.W., 2010. Controlling low-level image properties: the SHINE toolbox. *Behav. Res. Methods* 42, 671–684.
- Young, A.W., Perrett, D.I., Calder, A.J., Sprengelmeyer, R., Ekman, P., 2002. *Facial Expression of Emotion: Stimuli and Test (FEEST)*. Thames Valley Test Company, Bury St. Edmunds.
- Zotov, V., Jones, M.N., Mewhort, D.J.K., 2011. Contrast and assimilation in categorization and exemplar production. *Atten. Percept. Psychophys.* 73, 621–639.