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Report

Conscious Awareness of Flicker in Humans Involves Frontal and Parietal Cortex

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Summary

Even when confined to the same spatial location, flickering and steady light evoke very different conscious experiences because of their distinct temporal patterns. The neural basis of such differences in subjective experience remains uncertain [1]. Here, we used functional MRI in humans to examine the neural structures involved in awareness of flicker. Participants viewed a single point source of light that flickered at the critical flicker fusion (CFF) threshold, where the same stimulus is sometimes perceived as flickering and sometimes as steady (fused) [1–3]. We were thus able to compare brain activity for conscious percepts that differed qualitatively (flickering or fused) but were evoked by identical physical stimuli. Greater brain activation was observed on flicker (versus fused) trials in regions of frontal and parietal cortex previously associated with visual awareness in tasks that did not require detection of temporal patterns [4–14]. In contrast, greater activation was observed on fused (versus flicker) trials in occipital extrastriate cortex. Our findings indicate that activity of higher-level cortical areas is important for awareness of temporally distinct visual events in the context of a nonspatial task, and they thus suggest that frontal and parietal regions may play a general role in visual awareness.

Results

Subjective experience of the physical world depends not only on the spatial arrangement of the environment, but also on the temporal pattern of stimulation. For example, flickering and steady light can be presented in the same location yet evoke a very different conscious experience because of their different temporal patterns. The neural correlates of such temporally dependent aspects of conscious experience remain largely unknown. Recent studies show that visual awareness is associated not only with activity in occipital visual cortex but also in areas of frontal and parietal cortex [4–14]; and transient [15, 16] or permanent [17, 18] disruption of parietal- and frontal-cortex activity can lead to deficits in spatial awareness. The common involvement of these regions in diverse experimental paradigms suggests that they play a general role in visual awareness, and many studies have indeed suggested that attentional functions mediated by these regions are critical for awareness. However, it is not known whether activity in these areas is also associated with temporal aspects of subjective experience.

We therefore used event-related functional magnetic resonance imaging (fMRI) in humans to determine the neural correlates of conscious perception of flicker. Flicker is a rapid train of discrete luminance changes. When sufficiently fast, such luminance changes are no longer perceived as flickering but as steady, or fused, illumination [2, 3]. At the critical flicker fusion (CFF) threshold (~25–50 Hz [1–3]), a flickering light has an equal probability of being perceived as flickering or fused. Previous neuroimaging research on flicker has focused on the relationship between different flicker frequencies and brain activity [19–23]. In contrast, here we avoided confounding physical stimulation and perceptual outcome by characterizing brain activity associated with different conscious percepts (flickering or fused), but evoked by physically identical stimuli (flicker at the CFF threshold). Because neurons in early visual cortex can reflect frequencies far above the CFF threshold [24–29], we reasoned that perception of flicker at threshold frequencies would depend instead on activity in higher cortical regions. Specifically, fluctuations of attention-related activity in these higher-level regions might determine whether the same stimulus will lead to a flicker or fused percept. We therefore hypothesized that the frontal and parietal regions previously implicated in nontemporal aspects of awareness [4, 5] would also be involved in conscious awareness of flicker (see the Supplemental Data available online for specific predicted anatomic loci). We measured brain activity in 13 participants who responded on each trial to a single, foveated Light Emitting Diode (LED) flickering for 500 ms at one of three frequencies (the individually adjusted CFF threshold and threshold ± 1 Hz; see Experimental Procedures) by reporting whether or not they perceived the light to be flickering. Catch trials (with frequencies either much higher or lower than the CFF threshold) were used to control for response bias.

Behavior

Mean flicker-fusion threshold was 29.85 Hz across participants (range 24–35 Hz), and flicker percepts were reported on 41% of trials (range 29%–66%), so there were large numbers of both flicker and fused percepts for all participants. Performance on catch trials was nearly perfect, with 0.43 miscategorizations (range 0–3) for the 12 catch trials in each fMRI run. Participants

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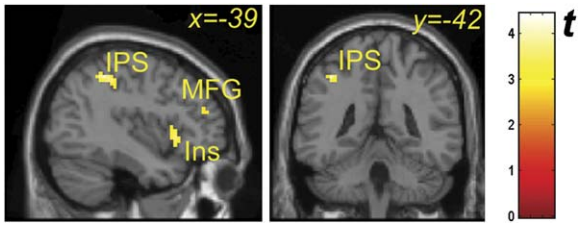

Figure 1. Flicker > Fused

A number of the frontal and parietal areas where event-related activity was greater for flicker than for fused percepts are superimposed on sagittal and coronal sections of a T1-weighted anatomical template image in MNI space. All peaks of activation reaching statistical significance are listed in Table 1. A statistical threshold of Z = 2.58 (corresponding to $p < 0.005$, uncorrected) and a cluster-size threshold of at least 10 voxels were used for display purposes in this and Figure 2. The MNI coordinate corresponding to the section's plane is indicated on each section. IPS denotes intraparietal sulcus, MFG denotes middle frontal gyrus, and Ins denotes insula.

were therefore attending to the task rather than responding randomly.

fMRI

A within-subject random-effects ANOVA was used to reveal brain areas associated with effects of percept (flicker or fused), frequency, and their interaction. In voxels where there was a significant effect of percept, t tests were used to determine its direction. Physically identical trials evoking flicker (versus fused) percepts were associated with greater activation in predicted parietal and frontal regions (Figure 1 and Table 1), e.g., intraparietal sulcus (Brodmann area 7 [BA7]); the inferior parietal lobule (BA40); the inferior (BA44), middle (BA46), and medial (BA6) frontal gyri; the anterior insula; and the cingulate sulcus (BA32). Activation was bilateral in frontal regions, but lateralized to the left in the parietal lobe. In contrast, fused percepts were associated with activation in several brain regions (Table 2 and Figure 2), especially occipital extrastriate cortex. Activation was bilateral, but the most significant activations were observed in the right hemisphere. No brain areas showed a significant main effect of frequency or an interaction between frequency and percept. This rules out the possibility that differential brain activity associated with flicker (versus fused) percepts could be due to the different frequencies used (see Experimental Procedures and Figure S1).

Eye Monitoring

Eye-monitoring data were available for eight of the 13 participants and showed no significant differences between flicker and fused percepts for either mean distance from fixation ($t_{(7)} = 0.832$, *ns*) or the standard deviation of distances ($t_{(7)} = 1.224$, *ns*). This rules out any effect of saccades or variance in eye position on our findings, but it remains possible that microsaccades or other fixational eye movements could contribute to our findings (see Supplemental Data for details). In contrast to the distance measures, pupil diameter was significantly greater on flicker (versus fused) trials ($t_{(7)} = 4.217$, $p = 0.004$). However, this effect was extremely small (a difference of ~0.05 mm, representing a change of ~2% in pupil area) and thus unlikely to result in differential activation in visual cortex. Indeed, activation in extrastriate cortex was lower, not higher, on trials in which flicker was perceived despite pupil diameter being slightly larger (Table 2). Importantly, the difference in pupil diameter was apparent from trial onset and remained similar in magnitude throughout the trial (as indicated by the first pupil-diameter measurement in a trial: $t_{(7)} = 4.667$, $p = 0.002$; and also by dividing the trial into 100 ms bins: flicker > fused in all bins, main effect of flicker versus fused $F_{(1,7)} = 18.28$, $p = 0.004$; all $t_{(7)}$ scores for the separate bins > 4.166, $p = 0.004$; no interaction between bin and percept, $F_{(1,7)} < 1$).

Discussion

Flickering and fused percepts were associated with distinct patterns of activation in response to physically identical flickering stimuli. Specifically, perception of flicker was associated with greater activation in bilateral frontal and left parietal cortex. This cortical network has previously been associated with awareness in tasks that did not specifically examine the temporal aspects of subjective experience in a nonspatial task, as studied here [4–18]. Our new findings demonstrate that these areas are also involved in awareness of temporal

Table 1. Loci and t Scores of Cluster Maxima in which There Was Significantly Higher Activation for Flicker Than for Fused Percepts

Region	Brodmann Area	Hemisphere	x	y	z	t Score
Inferior parietal lobule	40	L	−57	−30	39	4.42
Inferior frontal gyrus	44	L	−60	9	21	4.11
Intraparietal sulcus	7	L	−39	−42	48	3.94
Middle frontal gyrus	46	L	−45	45	18	3.80
Middle frontal gyrus	46	R	48	48	9	3.57
Anterior insula	—	R	30	24	0	3.75
Anterior insula	—	L	−39	18	−3	3.61
Cingulate sulcus	32	L	−6	30	30	3.75
Medial frontal gyrus	6	L	−12	−6	57	3.59
Parieto-occipital fisure	7	L	−12	−75	45	3.55
Superior frontal gyrus	6	R	21	−18	66	3.48

Coordinates are given in standard MNI space. Shown are significantly activated voxels in frontal and parietal cortex, at a threshold of $p < 0.001$, uncorrected (because of our prior hypothesis regarding these areas, see Supplemental Data). Even at this uncorrected threshold, there were only two foci of activation outside the predicted regions: in the medial aspect of the superior frontal gyrus (BA8), and in the postcentral gyrus (BA2). Only one of the predicted regions (BA9) contained no activated foci. R denotes right hemisphere; L denotes left hemisphere.

Table 2. Loci and t Scores of Cluster Maxima in which There Was Significantly Higher Activation for Fused Than for Flicker Percepts

Region	Brodmann Area	Hemisphere	x	y	z	t Score
Middle occipital gyrus	18/19	R	33	−90	15	5.52
Cuneus	18/19	R	9	−93	18	5.19
Cuneus	19	R	12	−87	36	4.33
Lateral occipital sulcus	18/19	R	42	−75	3	4.96
Fusiform gyrus	37	L	−36	−42	−15	4.83
Inferior frontal gyrus	45	R	54	30	12	4.61
Middle temporal gyrus	21	L	−57	−33	0	4.56
Middle temporal gyrus	21	L	−66	−27	−3	4.04
Cerebellum, posterior lobe	—	L	−24	−66	−21	4.56
Anterior occipital sulcus	18/19	L	−30	−75	−6	4.46
Postcentral gyrus	1	L	−39	−21	42	4.32
Insula	—	L	−30	6	18	4.24
Posterior transverse collateral sulcus	18/19	L	−21	−72	−6	4.46
Superior occipital gyrus	18/19	R	15	−102	6	4.15
Inferior occipital gyrus	18/19	R	30	−87	−15	4.14
Inferior occipital gyrus	18/19	R	18	−99	−6	4.10
Transverse occipital sulcus	18/19	R	30	−81	18	4.07
Transverse occipital sulcus	18/19	R	30	−84	9	4.04
Transverse occipital sulcus	18/19	R	39	−75	21	3.98
Cerebellum (vermis)	—		0	−63	−3	4.05

Coordinates are given in standard MNI space. Because we had no prior hypothesis regarding areas that would be activated when participants failed to detect flicker, we used a corrected threshold of $p < 0.05$ (FDR correction) for this contrast, as well as for the main effect of frequency and the interaction of frequency and percept, for which no significant activations were found (see fMRI section). R denotes right hemisphere; L denotes left hemisphere.

nonspatial properties of the visual environment and may therefore play a general role in visual awareness.

Patients with right parietal damage are impaired in temporal discrimination (distinguishing onsets from offsets), but have no impairment in detecting flicker [30]. This is consistent with our finding of left parietal activation for flicker detection. Taken together, these findings suggest that right parietal damage may be associated with the disruption of an attentional process devoted to relative timing [30] but not with the detection of temporal patterns, which may be functionally preserved in the intact left parietal lobe.

Neurons in visual cortex represent flicker at much higher frequencies than the CFF threshold [24–29], consistent with our finding that there was no interaction of frequency and percept (see Figure S1, Supplemental Data). Frontoparietal activity related to the percept of flicker may thus be associated with processes linked to awareness rather than sensory processing per se.

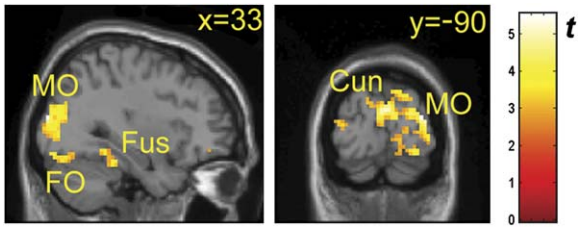

Figure 2. Fused > Flicker

Sagittal and coronal sections of a T1-weighted anatomical template image in MNI space, with superimposed areas where event-related activity was greater for fused than for flicker percepts. Most of this activity occurred in occipital extrastriate regions. The full list of activation peaks reaching statistical significance is given in Table 2. The following abbreviations are used: MO, middle occipital gyrus; FO, fourth occipital gyrus; Fus, fusiform gyrus; and Cun, cuneus.

Our findings are also consistent with theories of visual awareness in which awareness is constrained not by the properties of early visual neurons, but rather by a higher-level network comprising neuronal "coalitions" or serving as a "global neuronal workspace." In such views, consciousness arises from the interaction of widespread networks across the brain, rather than from activity in early sensory cortex [31–34].

Given that we used a single point source of light, shifts of spatial attention cannot account for these findings (unlike many previous studies of visual awareness [4–18]). However, our data also raise the intriguing and rather different possibility that nonspatial attention, known to be associated with frontoparietal activation similar to that found here [35], is involved in conscious flicker perception. Functional-imaging data cannot determine whether frontoparietal activation plays a causal role in flicker detection, or whether it results from such detection. For example, perceived flicker may attract attention automatically as a result of the sharp luminance onsets, and frontoparietal activity may reflect this. Alternatively, flicker detection may be facilitated when activity levels in frontoparietal cortex are high, consistent with a causal role for (nonspatial) attentional functions of the frontoparietal cortex in flicker awareness. Interestingly, the latter possibility is supported by our findings that flicker percepts were associated with a slightly larger pupil diameter from trial onset. Pupil dilation has previously been associated with attention and effort [36], and pupil dilation induced by task difficulty has been associated with activity in frontal and parietal regions [37]. We speculate that the difference in pupil size we observed may therefore result from cortical activity related to attentional effort in the flicker detection task, reflecting a pre-existing brain state that may have determined the perceptual outcome of each trial. Attentional effort may have fluctuated between trials, with

increases in attention leading both to better flicker detection and to pupil dilation. Importantly, attention would not be directed at spatial, but rather at temporal properties of the stimulus. Such a notion receives support from recent behavioral work showing that temporal parsing of visual input is sensitive to attentional manipulation [38–40]. The frontoparietal activity we found may reflect a general role of attention in enhancing the detection and selection of any target event (be it temporal or spatial), but it is important to note that because participants reported their percept on both flicker and fused trials, the ability to report the target cannot, in itself, account for observations of frontoparietal activity associated with flicker perception.

In contrast to conscious perception of flicker, fused percepts were predominantly associated with activation of occipital cortex. Foveal presentation of the flicker stimulus, plus our random-effects analysis (which necessarily averaged across participants), does not permit determination of the precise retinotopic location of these activations. However, they fall clearly outside the calcarine sulcus and therefore are likely to reflect activity in extrastriate visual cortex [41]. The finding of activated extrastriate foci for physically identical (though perceptually distinct) stimuli is surprising but clearly rules out the possibility that successful flicker detection relies on activity in early visual cortex (either instead of or in addition to the frontoparietal activity). It is well established that activity in visual cortex can more closely reflect phenomenal experience than physical stimulation [42, 43]. The present findings suggest that such differences in activity of visual cortex may extend to situations where phenomenally different experience arises from different temporal parsing of visual input.

Conclusions

Frontal and parietal cortex is involved in detecting flicker in a single, small point source of light. Given that activity in similar cortical regions has previously been associated with visual awareness in a variety of other tasks that have not involved detection of a temporal pattern, our findings suggest that frontal and parietal cortex may play an important general role in supporting visual awareness.

Experimental Procedures

Participants

Thirteen healthy volunteers (11 female, mean age 26.4, range 23–34) gave written informed consent to participate in the study, which was approved by the local ethics committee. All participants had normal or corrected-to-normal vision.

fMRI Scanning

A 3T Siemens Allegra system was used to acquire both T1-weighted anatomical images and T2-weighted echoplanar (EPI) images with blood-oxygenation-level-dependent (BOLD) contrast. For full details, see Supplemental Data.

Stimuli and Apparatus

Participants lay supine in the MRI scanner. On each trial, they fixated (through a mirror mounted on the head coil) a single red LED (CIE chromaticity coordinates $x = 0.655$, $y = 0.344$) subtending 0.2° visual angle, which flickered for 500 ms (square-wave flicker, 1:1 duty cycle; luminance 29 cd/m^2 at 30 Hz). Foveal presentation and brief duration minimized temporal adaptation effects [2]. Four fluorescent nonius lines (at right angles to each other in a "+" configuration) were placed around the LED to aid fixation. The room was completely dark apart from the LED and nonius lines. On each trial, participants reported by button press whether they perceived the light as flickering or not.

Behavioral-Threshold Measurement

To observe the neural correlates of the percept (flickering or fused) while keeping the physical stimulus constant, we first assessed the CFF threshold (the frequency at which a flickering light has an equal probability of being perceived as flickering or fused) for each participant. The CFF threshold was assessed at the beginning of the experimental session, in the scanner (but prior to scanning), by using the method of constant stimuli. For full details of the procedure, see Supplemental Data. The data obtained were used to estimate the participant's threshold frequency (the frequency at which the participant would be equally likely to categorize the stimulus as flickering or fused). This was rounded to the nearest whole number and then used to determine the frequencies displayed during scanning (see below).

MRI Scanning

In a preliminary behavioral study, we found that even when shown the preassessed threshold frequency, if only a single frequency was used in all trials, participants tended to adopt a constant response. In order to eliminate this tendency, we used three frequencies in our experimental conditions: the preassessed threshold (rounded to the nearest whole number) and frequencies 1 Hz lower and 1 Hz higher. Each flicker event lasted 500 ms. Null events, in which no stimulus appeared, were also included. There were an equal number of trials with threshold frequency, threshold minus 1 Hz, threshold plus 1 Hz, and null events. In addition, to further monitor for any response bias, we included a small number of catch trials in which the frequency was reliably above or below CFF threshold: either 8 Hz higher (5% of trials) or 8 Hz lower (5% of trials). For further details, see Supplemental Data.

Data Analysis

Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, University College London) was used to analyze the functional-imaging data. Standardized procedures were employed for preprocessing (see Supplemental Data for details). An event-related random-effects model was used for statistical analysis.

Eye-Position Monitoring

During scanning, eye position was continually sampled at 60 Hz by using long-range infrared video-oculography (ASL 504LRO Eye Tracking System, Massachusetts). For further details, see Supplemental Data.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and one figure and are available with this article online at: http://www.current-biology.com/cgi/content/full/16/9/907/DC1/.

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