The major brain networks of human visual consciousness

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Abstract

Understanding consciousness is one of the most important and challenging questions in modern science. Existing theories have pursued single unifying mechanisms but do not succeed in explaining consciousness. Importantly, the neural circuits that distinguish messages that arrive from the outside world and attain consciousness have remained unknown. Here we identify signals throughout the entire brain at high spatiotemporal resolution specifically related to consciousness. To accomplish this, we combined a large sample size of electrical and neuroimaging data with a novel experimental approach to remove confounding signal unrelated to consciousness\textsuperscript{1-3}. We discovered three major brain networks driving conscious visual perception. First, we found increases in signal detection regions in visual, fusiform cortex, and frontal eye fields; and in arousal/salience networks involving midbrain, thalamus, nucleus accumbens, anterior cingulate, and anterior insula. Second, we found increases in frontoparietal attention and executive control networks and in the cerebellum. Finally, we found decreases in the default mode network. Our results identify subcortical and cortical networks designed for signal detection, attentional amplification, and perceptual processing that together can explain visual consciousness. These findings provide evidence that understanding consciousness can be reframed as requiring multiple overlapping brain networks to produce consciousness of visual events\textsuperscript{4}. 
Main Text
Consciousness is central to human experience yet is not easily explained. Theories of consciousness typically emphasize a single mechanism hoping to solve the mystery linking brain activity to conscious experience. However, single-mechanism theories or models have so far not achieved convincing success. Instead, we posit that consciousness is best understood through a synergistic combination of multiple mechanisms overlapping in space and time. Just as several processes in biology together distinguish living from non-living things, multiple mechanisms in neuroscience combine to separate conscious from non-conscious neural activity. Specifically, conscious awareness of discrete events lies at the temporal nexus of attention and memory, both major fields in modern neuroscience that contribute to understanding consciousness. We hypothesize that systems crucial for consciousness include: (1) attention mechanism mediating signal detection, dynamic modulation of arousal, and bottom-up plus top-down attentional control, overlapping in space and time with; (2) systems that limit competing signals (e.g., through reduced default mode network activity); and, finally, (3) hierarchically organized systems that fully process signals for memory encoding and subsequent report.

To investigate these multiple systems, a comprehensive approach is needed to identify activity throughout the brain at high spatial and temporal resolution specifically related to consciousness. We aimed to overcome several limitations of prior studies. For example, subcortical regions are poorly understood in human conscious perception and are often relegated to preconscious state-based precursors of consciousness. We therefore investigated dynamic changes in both subcortical and cortical systems using techniques with complementary strengths. These included scalp electroencephalography (EEG) with large sample size and depth recordings from the human thalamus providing direct measurements of neural activity at high time resolution, and functional magnetic resonance imaging (fMRI) with large sample size analyzed with data-driven approaches providing comprehensive mapping of the whole brain. Most importantly for linking these neural measures with consciousness, we used a threshold visual perception task to measure brain signals produced by physically identical stimuli that are either perceived versus not perceived, coupled with a unique innovation to remove the confound of overt report. When participants are asked to overtly report whether they have perceived a stimulus this introduces post-perceptual processes (e.g., decision making and motor planning) that can confound signals linked to consciousness, even when the report is delayed by several seconds after the stimulus.

Identifying visual conscious perception without report
To address the confound of post-perceptual processing we developed a novel no-report paradigm using transient changes in pupillometry and eye tracking to classify stimuli as perceived or not perceived without overt report (fig. S1-9; Tables S4-6). In a previously established Report Paradigm, participants were repeatedly shown identical faces at 50% perceptual threshold (Fig. 1A). This resulted in approximately equal numbers of perceived and not perceived stimuli based on overt report of stimulus presence and location (fig. S6, 7). We formed a novel combined Report + No-Report Paradigm by maintaining the report, task-relevant stimuli from the Report Paradigm and introducing identical no-report, task-irrelevant faces (i.e., stimuli that did not require overt report) interleaved with task-relevant stimuli, distinguished by different screen locations (four quadrant locations and four central locations; Fig. 1B). For example, in one session participants were told to report only on stimuli appearing in the screen quadrant locations and not in the screen central locations (fig. S1A; see for counterbalancing and details). The perception of no-report stimuli was determined by classification of pupillometry and eye tracking.
during the task. Specifically, we found pupil dilation, blink rate increases, and microsaccade rate
decreases for consciously perceived visual stimuli, present irrespective of task relevance (Fig.
1C, D). Pupillometry and eye tracking have been previously implemented as covert measures of
consciousness. However, the dynamics reported here are unique because they do not rely on
a task sequence (e.g., no-report stimuli always first), changes in the stimulus (our stimuli are
all identical), perceptual switching (e.g., binocular rivalry), nor stimulus type (e.g., stimulus
modality), as we have found similar pupil, blink, and microsaccade responses for perceived
auditory and tactile stimuli.

Report-independent event-related potentials in conscious visual perception
Our first goal was to investigate report-dependent and report-independent brain signals at high
time resolution. We recorded the following well established event-related potentials (ERPs) for
perceived stimuli in the report data, in temporal sequence: (1) N100, (2) VAN (visual awareness
negativity), (3) P2/N2, and (4) P3/LP (late potentials) (Fig. 2A; fig. S10A, 11A). The earliest
ERP (N100) is thought to be related to visual cortical activation, and was present for all stimuli
regardless of perceived, not perceived, report or no-report, although the magnitude varied
depending on conditions (fig. S10, 11). The VAN was significantly greater for perceived versus
not perceived stimuli, both for report and no-report data (Fig. 2A, B; fig. S10A, C). Importantly,
the VAN was not significantly different for report versus no-report data, whereas the later ERPs
(P2/N2 and P3/LP) were significantly larger for perceived stimuli in the report data (Fig. 2C; fig.
S10E). Our novel paradigm thus strengthens previous findings that early ERPs, particularly the
VAN, are seen even under no-report or task-irrelevant conditions. Therefore, these early signals
reflect the scalp neurophysiological signatures for report-independent conscious perception. Furthermore, report and task-relevance introduce report-dependent changes dominated by later
ERPs, including P3/LP that extend persistent neurophysiological activity for over 1 second after
stimulus onset (fig. S11A; see also and fig. S9 in).

Thalamic awareness potential
Having established early report-independent signals of conscious perception, and later report-
dependent signals likely related to post-perceptual processing, we next sought to investigate
subcortical signals selective for conscious perception and to determine their timing. A key
subcortical brain structure for arousal and consciousness is the intralaminar thalamus. Patient
participants with chronically implanted deep brain recording and stimulation devices (RNS®
System, NeuroPace, Inc.; Natus NeuroWorks, Inc.) for the treatment of epilepsy provided unique
access to this region. We simultaneously recorded cortical electrophysiology from scalp EEG
and subcortical signals from thalamic depth contacts (Fig. 2D; fig. S12, 13; Tables S2, 3) while
participants completed the Report Paradigm. We found a novel, biphasic thalamic awareness
potential (TAP) highly selective for perceived stimuli with an onset at ~250ms and initial peak at
~430ms post-stimulus presentation (Fig. 2E). TAP was localized to channels within or along the
lateral border of the intralaminar thalamus (Fig. S2D; fig. S12). TAP was also selectively present
for perceived auditory stimuli in one participant (participant 1 in Table S2) who completed an
analogous perceptual threshold auditory task in a separate study from our group (fig. S14).

We next investigated the timing of TAP relative to scalp ERPs. First, we noted that the
scalp ERPs recorded in the patient participants were similar to those of the healthy participants,
despite different recording systems and sample sizes (fig. S13). We found that TAP preceded P3,
but followed the N100, VAN, and N2 (Fig. 2F). Therefore, the timing of TAP was later than
ERPs found in the prior experiment to be report-independent (VAN), and fell within or earlier
than ERPs that were report-dependent (N2, P3). We did not directly test whether TAP was report-dependent because of limited recording time with the patient participants. However, because we hypothesized that TAP is one node in a broad subcortical arousal and salience network participating in attention state dynamics and consciousness, we next used fMRI in a large cohort of healthy participants to investigate cortical and subcortical conscious perception-linked dynamics, with and without overt report.

Report-independent fMRI changes in conscious visual perception

We found a broad network of subcortical and cortical regions showing report-independent fMRI changes especially at earlier times after stimulus presentation. Perceived versus not perceived blood-oxygen-level-dependent (BOLD) responses were distinguished by early (<4 seconds) and late (>5 seconds) dynamics analyzed by spatiotemporal cluster-based permutation tests. At 3 seconds post-stimulus (Fig. 3A, C; fig. S15A, C; Slide S1, 2), report-independent increases were shared by both report and no-report data in signal detection regions, including primary visual cortex (V1), fusiform gyrus (FG), and the posterior middle frontal gyrus (PMFG; near to the frontal eye fields, FEF). Additional report-independent subcortical and cortical increases were found at early times in arousal and salience networks, including the midbrain tegmentum (MT), thalamus (Th), nucleus accumbens (NA), anterior cingulate/supplementary motor area (AC/SMA), and anterior insula/claustrum (AI). Finally, shared report-independent increases at early times were seen in attention and executive control networks, including the anterior inferior parietal lobule (AIPL), dorsal inferior parietal lobule (DIPL), superior parietal lobule (SPL), medial parietal cortex (MP), anterior middle frontal gyrus (AMFG), frontal pole (FP), and cerebellum (Crus I, II).

In contrast, at 6 seconds post-stimulus and later there were fewer shared report-independent regions seen in both report and no-report data (Fig. 3B, D; fig. S15B, D; Slide S1, 2). Most shared changes at 6 seconds involved decreases in default mode network (DMN) areas, including the ventral medial prefrontal cortex (VMFC), posterior cingulate/precuneus (PC), posterior inferior parietal lobule (PIPL), and anterolateral temporal cortex (ALT). Shared increases at 6 seconds were limited to few and relatively small regions of V1, cerebellum, frontoparietal cortex, and Th. At the same time, the report data alone showed prominent persistent or peak increases at 6 seconds in attention and executive control networks, including AIPL, SPL, MP, AMFG, orbital frontal cortex (OFC), FP, striatum (Str), and cerebellum, as well as, more prominent decreases in DMN regions (Fig. 3B; fig. S15B; Slide S1).

Conjunction analyses emphasize the broad shared report-independent networks seen mainly at earlier times in fMRI including regions important for signal detection, arousal, salience, attention, and executive control, as well as, some involvement of DMN (Fig. 3E, F; Slide S4). Report versus no-report statistical comparisons with cluster-based permutation tests (p < 0.05) of perceived minus not perceived fMRI signal show greater differences at later times, including in left cortical motor regions, possibly linked to motor planning for subsequent right-hand behavioral responses (fig. S16A, B; Slide S3). Likewise, analysis of signals significant only in report (fig. S16C, D; Slide S5) highlighted the separate report-dependent regions such as motor cortex, OFC, Str, and PC, not significantly involved at any time in no-report data, as well as, attention, executive, and cerebellar regions that were shared at early times, but remained persistently activated only in the report data. Analysis of signals significant only in no-report data found early increases in sensory regions (e.g., V1 and FG) that are unique to the no-report network (fig. S16E, F; Slide S6).
Major cortical and subcortical networks in conscious visual perception

To further investigate the main large-scale networks involved in conscious perception with and without report and the temporal profile of these networks, we used temporal correlation-based k-means clustering across the entire brain. Data-driven clustering of statistically significant voxels for report perceived versus not perceived fMRI signals revealed three anatomically and functionally distinct networks: (1) early positive, (2) late positive, and (3) late negative (Fig. 4A-F; fig. S17D, E, F). The early positive network has a peak at 3-4 seconds after stimulus onset and includes subcortical and cortical detection, arousal, and salience networks (DAS). They include FG, PMFG, MT, Th, NA, AC/SMA, AI, cerebellar vermis, and subregions of the Str, AIPL, SPL and MP (Fig. 4A). The late positive network peaks ~6 seconds after stimulus onset and includes task-positive networks (TPN) such as AMFG, OFC, FP, cerebellum Crus I and II, and subregions of the Str, AIPL, SPL, and MP (Fig. 4B). The late negative network has a trough at 6-8 seconds after stimulus onset and occupies DMN regions that are exclusively cortical, including the VMFC, PC, PIPL, and ALT (Fig. 4C). Thus, three major and distinct brain networks for conscious perception emerge from the fMRI data entirely based on BOLD timecourse dynamics.

How does overt report change the signal timecourses in these networks? Analysis of mean timecourses for all voxels within each network revealed that only TPN was on the whole different between report and no-report data at later times (Fig. 4D-F). However, subregion analyses showed that all three networks contained both regions that agreed and regions that differed between report and no-report data (Fig. 4G-J; fig. S18-20). Importantly, the fMRI timecourse for Th (>94% DAS voxels) did not differ between report and no-report conditions (Fig. 4G). In contrast, the PMFG/FEF (>87% DAS voxels), DIPL (>82% TPN voxels), and VMFC (>79% DMN voxels) had greater signal amplitude and duration for report versus no-report conditions (Fig. 4H-J). Similar to the conjunction and difference analyses already discussed (Fig. 3E, F; fig. S16), additional timecourse analyses confirmed that some brain areas (e.g., left motor cortex; fig. S19) are only significantly involved in report data, whereas many more regions are shared between report and no-report data at early times, but show persistent or larger signals in report data at later times (e.g., DIPL, SPL, MP; fig. S18-20).

Discussion

We found that multiple mechanisms at the nexus of attention, signal processing and memory formation contribute to conscious visual perception. Report-independent signals are early and transient, and on EEG include the N100 and VAN. Report-independent signals from fMRI with the identical behavioral paradigm and many of the same participants as EEG, showed early and transient, but widespread involvement of three major subcortical and cortical brain networks. The importance of subcortical networks in conscious perception was further supported by our identification of the TAP through direct recordings from the human thalamus. Meanwhile, report-dependent signals were late and persistent, and on EEG include the P2/N2 and P3/LP; and late (~6 seconds) fMRI signals in DAS, TPN, and DMN. Persistent BOLD signals for report data may be linked to prolonged neuronal activity changes needed for subsequent report, manifested electrophysiologically as late potentials (fig. S11A), or other sustained activity following perception.

These findings support an approach to studying consciousness based on investigation of multiple overlapping systems in neuroscience, rather than looking for a single theoretical model. This approach has succeeded in the study of other important and complex biological functions.
(e.g., reproduction and digestion) where no single model is proposed, and instead multiple contributing processes are found that provide key features. Our identification of specific report-independent subcortical and cortical systems overlapping in space and time is an important step forward towards understanding the neural mechanisms of consciousness. These systems can be placed along a proposed timeline consistent with the three major networks found in our data. First, (1) Detection/arousal/salience (DAS): when a visual stimulus appears, activation of V1 interacts with FG, FEF, and other regions for signal detection. A dynamic transient pulse in subcortical arousal (e.g., MT and Th) and emotional/motivational systems (e.g., NA) amplifies and facilitates bottom-up attentional salience and top-down attentional control. Next, (2) Default-mode network (DMN): switching off of the DMN and related circuits can reduce competing signals to prevent interference with conscious perception. Finally, (3) Task-positive networks (TPN): a broad wave of hierarchical processing sweeps through task-positive cortical and subcortical areas to fully process the event before it is encoded in working and episodic memory systems. The later events along this timeline, especially for TPN, merge into report-dependent, post-perceptual processing needed for subsequent report. Overall our present results agree with recent work suggesting that visual perception begins with early signal detection followed by a pulse of arousal, attentional and limbic signal amplification leading to network switching and a wave of processing to form conscious experiences.

Brain mechanisms of conscious visual perception are early, transient, and large-scale. The spatiotemporal signatures of conscious perception suggest that the human brain produces consciousness using synergistic and redundant systems, combining signal detection, attentional amplification, selective information control and processing. A large and layered neural architecture would be advantageous by making the conscious network resistant to damage or change. Investigating these rich and complex overlapping systems may provide a satisfactory explanation for consciousness.

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Materials and methods are available as supplementary materials.

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Fig. 1. Report-dependent and report-independent behavioral paradigms for conscious perception; similar pupillometry and eye tracking responses. (A) Report Paradigm trial sequence, stimulus locations, and opacity conditions. (B) Report + No-Report Paradigm trial sequence, stimulus locations, and opacity conditions. (C) Report (task-relevant) data with perception based on overt participant responses and (D) no-report (task-irrelevant) data with
perception classified by machine learning yield similar pupil, blink, and microsaccade dynamics
8. Data in (C) and (D) are from stimuli at perceptual threshold (see inset) in the Report + No-
Report Paradigm (N = 68 participants). Stimulus onset was at time = 0. Classification score
threshold for (D) was 0 (fig. S9) 37. Statistically significant (Statistically Sig.) different time
points between perceived and not perceived data are indicated (black bars above pupil, blink, and
microsaccade timecourses) based on cluster-based permutation tests (p < 0.05) 8. Standard error
of the mean (SEM).
Fig. 2. Cortical and thalamic electrophysiology signals in conscious perception. (A-C) Scalp topographical plots of high-density EEG showing mean voltage for all statistically significant samples by cluster-based permutation tests ($p < 0.05$) in four time windows corresponding with the event-related potentials (ERPs) N100 (75-125ms), visual awareness negativity (VAN; 175-225ms), P2/N2 (275-325ms), and P3 (350-650ms) for perceived versus not perceived stimuli in (A) report, (B) no-report, and (C) report versus no-report data. The VAN is present both for...
report and no-report data, whereas later ERPs, especially N2 and P3 are report-dependent. (D) Subcortical depth channel locations collapsed onto a coronal slice (-19.9mm) in MNI brain template space. Red/purple (N = 13) and white bipolar channels (N = 11) distinguish above or below voltage threshold channels, respectively (fig. S12). Red channels are with the RNS System (NeuroPace, Inc.) and purple channels with Natus NeuroWorks (Natus, Inc.) depth electrode recordings (Table S2). Neighboring anatomy includes lateral ventricles (LV), third ventricle (3rd V), thalamus (Th), midbrain tegmentum (MT), and pons. (E) Thalamic awareness potential (TAP) and P3 are seen, respectively in thalamic above-threshold contacts and Pz (location on inset) scalp EEG contacts. Mean timecourses show significant differences for perceived versus not perceived stimuli in the ERP analysis for TAP and P3 by cluster-based permutation tests (*p < 0.05). Stimulus onset was at time = 0. (F) Peak latencies from stimulus onset for scalp ERPs and TAP. Circles represent individual data (mean channel latencies) and error bars indicate standard error of the mean (SEM). Significantly different latencies from TAP found by Wilcoxon rank sum test with Holm-Bonferroni correction (*p < 0.05). (A-C) Data for report stimuli are from Report Paradigm (N = 57) and Report + No-Report Paradigm (N = 65); data for no-report stimuli are from Report + No-Report Paradigm (N = 65). (D-F) Data are from Report Paradigm in patient participants with thalamic depth electrodes (N = 7).
Fig. 3. Whole brain fMRI maps for conscious perception with and without overt report. (A, B) Report and (C, D) no-report perceived minus not perceived statistically significant voxels from cluster-based permutation tests ($p < 0.05$) at 3 and 6 seconds post-stimulus presentation. Statistically significant positive and negative voxel cluster $t$-values are shown in warm and cool.
colors, respectively. Anatomical regions are labeled at their peak response between the 3 and 6-second time points. (E, F) Voxel-level conjunction analysis of report and no-report, perceived minus not perceived statistical whole brain maps with shared (report-independent) increases shown in green and shared decreases shown in purple. Pontine tegmentum (PT), midbrain tegmentum (MT), thalamus (Th), nucleus accumbens (NA), striatum (Str), anterior insula/claustrum (AI), anterior cingulate (AC), supplementary motor area (SMA), primary visual cortex (V1), fusiform gyrus (FG), anterior middle frontal gyrus (AMFG), posterior middle frontal gyrus (PMFG), frontal eye fields (FEF), frontal pole (FP), orbital frontal cortex (OFC), ventral medial prefrontal cortex (VMFC), anterior inferior parietal lobule (AIPL), dorsal inferior parietal lobule (DIPL), posterior inferior parietal lobule (PIPL), superior parietal lobule (SPL), medial parietal cortex (MP), posterior cingulate/precuneus (PC), and anterolateral temporal cortex (ALT). See Slides S1, 2, and 4 for all times 20 seconds pre and post-stimulus presentation for report, no-report, and conjunction results. Data for report stimuli are from Report Paradigm (N = 34) and Report + No-Report Paradigm (N = 65); data for no-report stimuli are from Report + No-Report Paradigm (N = 65).
Fig. 4. Data-driven anatomical clustering of fMRI signals for conscious perception and region of interest (ROI) timecourses. (A-C) Three large-scale networks found with k-means clustering based on fMRI timecourses (fig. S17). (A) detection, arousal, and salience networks (DAS), (B) task-positive networks (TPN), and (C) default mode network (DMN). Cortical and subcortical/cerebellar territories are shown in different shades. (D-F) Mean percent change blood-oxygen-level-dependent (BOLD) timecourses for report (green) and no-report (purple) perceived minus not perceived conditions for DAS, TPN, and DMN. (G-J) Selected subregion mean percent change BOLD timecourses (see also fig. S18-20). Percentages of voxels from a particular network (DAS, TPN, or DMN) versus all network voxels found in each ROI are shown for report (green) and no-report (purple) data. (K) Anatomical visualization of subregion ROIs from G, H, I, and J. Pontine tegmentum (PT), midbrain tegmentum (MT), thalamus (Th),
nucleus accumbens (NA), striatum (Str), anterior insula/claustrum (AI), anterior cingulate (AC), supplementary motor area (SMA), primary visual cortex (V1), fusiform gyrus (FG), anterior middle frontal gyrus (AMFG), posterior middle frontal gyrus (PMFG), frontal eye fields (FEF), frontal pole (FP), orbital frontal cortex (OFC), ventral medial prefrontal cortex (VMFC), anterior inferior parietal lobule (AIPL), dorsal inferior parietal lobule (DIPL), posterior inferior parietal lobule (PIPL), superior parietal lobule (SPL), medial parietal cortex (MP), posterior cingulate/precuneus (PC), and anterolateral temporal cortex (ALT). Stimulus onset was at time = 0. Data for report stimuli are from Report Paradigm (N = 34) and Report + No-Report Paradigm (N = 65); data for no-report stimuli are from Report + No-Report Paradigm (N = 65).
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**Data Availability:** All data is available in the manuscript or the supplementary materials. Data are available at http://kronemer-blumenfeld-data.yale.edu <<Note: this URL will be open at the time of publication>>

**Additional Information:**

**Supplementary Information** is available for this paper.

Correspondence and requests for materials should be addressed to Hal Blumenfeld.

**Extended Data**

Extended Data Slides S1 to S6
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