

Annual Review of Neuroscience Neuroscientific Evidence for Processing Without Awareness

Liad Mudrik¹ and Leon Y. Deouell²

¹School of Psychological Sciences and Sagol School of Neuroscience, Tel Aviv University, Tel Aviv, Israel; email: mudrikli@tauex.tau.ac.il

²Department of Psychology and The Edmond and Lily Safra Center for Brain Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel; email: leon.deouell@mail.huji.ac.il

Annu. Rev. Neurosci. 2022. 45:403-23

The Annual Review of Neuroscience is online at neuro.annualreviews.org

https://doi.org/10.1146/annurev-neuro-110920-033151

Copyright © 2022 by Annual Reviews. All rights reserved

ANNUAL CONNECT

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Keywords

processing without awareness, subliminal, fMRI, EEG/MEG, intracranial recordings, TMS

Abstract

The extent to which we are affected by perceptual input of which we are unaware is widely debated. By measuring neural responses to sensory stimulation, neuroscientific data could complement behavioral results with valuable evidence. Here we review neuroscientific findings of processing of high-level information, as well as interactions with attention and memory. Although the results are mixed, we find initial support for processing object categories and words, possibly to the semantic level, as well as emotional expressions. Robust neural evidence for face individuation and integration of sentences or scenes is lacking. Attention affects the processing of stimuli that are not consciously perceived, and such stimuli may exogenously but not endogenously capture attention when relevant, and be maintained in memory over time. Sources of inconsistency in the literature include variability in control for awareness as well as individual differences, calling for future studies that adopt stricter measures of awareness and probe multiple processes within subjects.

INTRODUCTION	404
OBJECT PROCESSING	407
LANGUAGE	411
EMOTION	412
ATTENTION	413
MEMORY	415
CONCLUSIONS	416

INTRODUCTION

For millennia, humans have been documenting their conscious experiences, be it with cave drawings, written words, or more modern forms of art. Unconscious processes became an explicit object of thought and research much later; the term unconscious was only introduced during the eighteenth century (Schelling 1993) and has been the focus of ongoing research and debate ever since. Understanding the scope of unconscious processes is important for any account of human behavior, as well as for theories of consciousness that make predictions about the functional difference between conscious and unconscious processing, such as global neuronal workspace theory (Dehaene & Naccache 2001) or recurrent processing theory (Lamme 2020).

In this review, by unconscious processing we are not referring to the Freudian unconscious (Freud 2005), to neural computations to which we simply do not have access (e.g., homeostatic processes), nor to the distinction between implicit and explicit processing (e.g., Maresch et al. 2021), which denotes the agent's awareness of the internal cognitive/affective/evaluative processing of external information (e.g., having attitudes toward someone, or learning a sequence, without being aware of it). Rather, we focus on the processing of information regarding a stimulus to which we have no conscious access. As a shorthand, we refer to such processing as processing without awareness. This term refers to processing of generally perceivable stimuli (like images of objects or printed words) that are not consciously perceived due to some experimental manipulation. Processing is then deduced from an effect of a not consciously perceived (NCP) stimulation on behavior or neural activity, in a way that suggests that its content has been processed.

How can neuroscience inform the attempt to understand processing without awareness? First, in providing evidence for stimulus-specific processing and delineating its scope, neuroscientific data complement and sometimes go beyond behavioral data or, in some cases, can be the only source of evidence even when no behavioral effects are found (e.g., Fahrenfort et al. 2017, van Gaal et al. 2014) or when the experimental logic does not allow the collection of behavioral evidence [e.g., when the stimuli should be task irrelevant (Pitts et al. 2012)]. It could be argued that a neural effect devoid of a behavioral effect could be meaningless in terms of brain function (an epiphenomenon). Yet, in some cases, neural data may be more sensitive than the behavioral task and thus should, in our view, serve as evidence for processing without awareness, as long as the activity is discriminatory and content specific.

Such discriminatory neural evidence can come in different forms: a response previously associated with specific processing of consciously perceived stimuli (neural signature), which is also evoked by NCP stimuli, or differential activation to two subliminal stimuli. Although the former involves an inverse inference (inferring function from neural activity) (Poldrack 2006), in some cases this seems justified given extensive multimodal research with supraliminal stimuli [e.g., the

Global neuronal

workspace: a theory suggesting that consciousness depends on global broadcasting of information across the brain by a specialized network

Recurrent processing theory:

a theory suggesting that consciousness depends on recurrent projections within low-level sensory areas electrophysiological component N170 or the functional MRI (fMRI) activation of the fusiform face area (FFA), for processing of faces]. Above-chance decoding is increasingly used as evidence for differential processing, though in most studies, classification is not much higher than chance. Thus, such inference should be taken with caution and might benefit from additional types of evidence such as neural perturbation.

A second contribution by neuroscience is the ability to track unconscious processes over time and space. Especially intriguing are cases where those differ from conscious processing. That is, most of the evidence reviewed below relies on finding similar (albeit often weaker) patterns for processing with and without awareness. Yet in some cases the patterns might involve different neural generators or show reversed patterns (e.g., positive electrophysiological components during conscious processing and negative ones during processing without awareness). Such different patterns imply that some unconscious processes might be qualitatively—and not only quantitatively different from analogous conscious processes.

Experimentally, studying processing without awareness entails two immediate challenges: demonstrating processing and ruling out awareness. A myriad of methods have been developed to meet the first challenge of presenting stimuli so they are not consciously perceived but still potent enough to evoke a meaningful neural response (for reviews, see Breitmeyer 2015, Kim & Blake 2005) (**Figure 1**), yet most involve tampering with the stimuli in different ways, inevitably evoking weaker signals. The second challenge of making sure that the stimuli are indeed not consciously perceived is a key issue that is still debated (e.g., Rothkirch & Hesselmann 2017, Shanks 2017). It is commonly assumed that to conclude that subjects were not aware of the stimuli, they should both report not perceiving it (subjective measure) and be at chance in making a direct explicit judgement about it (objective measure) (Merikle & Reingold 1998). Yet this approach brings about further complications of over- or underestimating consciousness (see the sidebar titled Methodological Challenges), leading, respectively, to type 2 (missing processing without awareness when it exists) or type 1 (concluding processing without awareness when none exists) statistical errors.

Numerous studies have reported the effect of NCP stimuli on behavior, or lack thereof. Here, we only focus on studies in which the evidence involves the brain, reporting differential activations evoked by stimuli that were behaviorally shown to have not been consciously perceived. In this nonexhaustive review, we aim to include studies with relatively sound measures of awareness. However, few studies are perfect in that sense, and we highlight the limitations. The reviewed studies include in-lab experiments on healthy subjects as well as patients with brain lesions, like blindsight or neglect. The latter studies typically include one or a few patients, which may again increase both type 1 and type 2 errors. Also, most of these studies typically do not use strict measures of awareness. Still, they often present striking dissociations between conscious perception and perceptual processing, obtained using salient, easy-to-perceive stimuli, as opposed to most studies with healthy subjects, which must substantially degrade or mask the stimuli to hamper awareness. We mostly excluded studies in disorders of consciousness such as coma or unresponsive wakefulness syndrome as well as sleep studies, given the difficulty in assessing the actual level of consciousness to external stimulation.

In the following, we review the current evidence for different types of relatively high-level processing of NCP stimuli (for the types of findings that commonly serve as evidence, see **Figure 2**). Numerous studies have also reported more low level, feature-specific responses evoked by such stimuli, including color (e.g., Zou et al. 2016), orientation and contour integration (e.g., Pitts et al. 2012), and motion (e.g., Moutoussis & Zeki 2006). Similar effects have also been found in the auditory (e.g., Sculthorpe et al. 2009), tactile (e.g., Forschack et al. 2020), and vestibular (e.g., Ganesh et al. 2018) domains. Here, we ask whether this also extends to higher-level processing and related faculties like attention or memory.

Subjective measure:

awareness assessment based on subjects' report of what they perceived, either binary (see/did not see) or using levels (e.g., no experience, brief glimpse, clear perception)

Objective measure:

awareness assessment based on subjects' performance on a forced-choice task (e.g., detection, discrimination) regarding the not consciously perceived stimulus

Blindsight: cortical blindness due to primary visual cortex lesions, where patients are still able to detect or discriminate features of stimuli in the blind field

Unilateral neglect

(UN): unawareness of contralesional stimuli independent of sensory deficits, usually due to right hemisphere lesions



Figure 1 (Figure appears on preceding page)

Methods used to render visual stimuli not consciously perceived. (a) Masking. A brief stimulus is immediately replaced (and sometimes sandwiched) by a mask. Panel adapted from Faivre et al. (2019) (CC BY 4.0). (b) Continuous flash suppression. The dominant eye is presented with dynamically changing patterns, suppressing the information presented to the nondominant eye. Panel adapted from Tettamanti et al. (2017) (CC BY 4.0). (c) Dichoptic fusion. By presenting opposite yet complementary patterns or colors to the two eyes, a uniform pattern is perceived, while each eye is presented with a distinct stimulus (here, a face). Panel adapted from Fahrenfort et al. (2012). (d) Stimulus degradation. The stimulus is presented in subthreshold contrast or embedded in noise. Here, the threshold contrast level of the circle was assessed individually to determine the required contrast for subliminal/supraliminal presentation. Panel adapted with permission from Bareither et al. (2014). (e) Inattentional blindness. While subjects are engaged in an attention-demanding task (here, concerning the *red circles*), task-unrelated stimuli (here, *square*) go unnoticed. Panel adapted with permission from Pitts et al. (2014). (f) Attentional blink. A series of stimuli are presented rapidly (every ~100 ms), and two of these stimuli are defined as targets that the subjects are asked to detect. When the first target precedes the second one by 200–600 ms, the second target is often missed. Panel adapted with permission from Reber et al. (2017). (g) Crowding. When gaze is centrally fixed, a peripheral stimulus surrounded by flankers is not consciously perceived. Panel adapted with permission from Faivre et al. (2017). (g) Crowding. When gaze is centrally fixed, a peripheral stimulus surrounded by flankers is not consciously perceived. Panel adapted with permission from Faivre et al. (2012). Abbreviation: ISI, interstimulus interval.

METHODOLOGICAL CHALLENGES

Confirming processing of not consciously perceived (NCP) stimuli requires demonstrating both processing and lack of conscious awareness, each entailing nontrivial challenges. Subjective awareness is best measured not by a binary yes/no question but by allowing subjects to grade their perception from "nothing" through "a glimpse" and up to full awareness (Perceptual Awareness Scale) (Sandberg et al. 2010). Some scholars also require a direct objective task like a two-alternative forced choice, ruling out above-chance guessing, as evidence for unawareness. However, good guessing may reflect unconscious, not only conscious, processing. When unawareness is tested is also important: A delayed awareness test relative to stimulus may reflect memory failure rather than unawareness. Demonstrating that processing indeed occurred involves other challenges: Neuroimaging analysis is fraught with statistical pitfalls, including the multiple comparisons problem (MCP): Determining significance at multiple points in time/space inflates the chance for erroneously finding an effect (type I error). Solutions to the MCP vary in level of control for a type I error. Typically, NCP stimuli evoke relatively weak neural responses and, accordingly, low signal-to-noise ratios and potentially spurious results. This reduces the statistical power, increasing both type I and type II (missing a real effect) errors. The solution could include increasing the number of trials, increasing the number of subjects, and, given the typically small effects, preregistered replications of experiments.

OBJECT PROCESSING

Overall, neuroscientific studies suggest that processing without awareness also encompasses semantic information, at least for simple, isolated stimuli. This was widely studied for faces, using their well-established neural correlates, including the N170 event-related potential (ERP) and face-selective regions like the fusiform and occipital face areas (Bentin et al. 1996, Haxby et al. 2000). Several studies found selective fMRI-based activations (e.g., Fahrenfort et al. 2012, Jiang & He 2006, Kouider et al. 2009), though others did not (Fang & He 2005, Rodríguez et al. 2012). A similar heterogeneity also characterizes electrophysiological findings: The N170 effect or its MEG counterpart, the M170, is sometimes found for NCP stimuli, though often weaker than during conscious processing (e.g., Harris et al. 2013, Sterzer et al. 2009, Suzuki et al. 2014). Yet in other studies, the N170 was only found for consciously perceived faces (e.g., Rodríguez et al. 2012, Shafto & Pitts 2015). One study found that although both inverted and upright faces elicit an N170, only upright faces do so when not consciously perceived (Suzuki & Noguchi 2013). This finding suggests that unconscious processing may be limited to well-trained stimuli, whose

N170: event-related potential component showing greater negativity for faces compared with other stimuli at ~170 ms poststimulus presentation



(Caption appears on following page)

408 Mudrik • Deouell

Annu. Rev. Neurosci. 2022.45:403-423. Downloaded from www.annualreviews.org Access provided by 192.114.23.221 on 08/11/23. See copyright for approved use.

Types of findings used as evidence for unconscious processing. (a) Differential activity. A not consciously perceived (NCP) stimulus elicits activity that is different from baseline or from another subliminal stimulus. Panel adapted with permission from Vandenbroucke et al. (2014). (b) Activation of specialized modules. An area with an already-established selectivity is also active during the processing of relevant NCP information [here, the fusiform face area (FFA) and superior temporal sulcus (STS) regions of interest (ROIs), defined in a separate localizer, are activated by NCP faces]. Panel adapted with permission from Jiang & He (2006). (c) Elicitation of specific event-related potential (ERP) components. An electrophysiological component that is linked with a known process is also active during unconscious processing: for example, finding (i) the mismatch negativity (MMN) to deviant stimuli during sleep (subpanel adapted with permission from Sculthorpe et al. 2009), (ii) N400 following a pair of masked words (subpanel adapted with permission from van Gaal et al. 2014), (iii) M170 for invisible faces (subpanel adapted from Sterzer et al. 2009), or (iv) a lateralized readiness potential (LRP) during early sleep stages (subpanel adapted from Kouider et al. 2014). (d) Repetition suppression. Response to a consciously perceived stimulus is reduced when it follows presentation of an identical or similar not consciously perceived stimulus. In this example, repetition suppression is present (colored pixels) when the repeated words are physically identical (both in Japanese Kanji, left) or written in different orthographic systems (Kanji and Kana, right) although the latter is more limited. Panel adapted with permission from Nakamura et al. (2005). (e) Decoding. Relevant information about a NCP stimulus can be classified from neural activation (here, target presence versus absence) whether perceived consciously (visibility 3) or not (visibility 0) (King et al. 2016). (f) Semantic priming following NCP stimuli. Patients with neglect are presented with a target that follows an image (prime) presented in their neglected left visual field [LVF, as opposed to the right visual field (RVF)] with an interstimulus interval (ISI) of 400 ms. Here, patients perform faster on deciding that "ball" is a word when first presented with an image of a baseball bat in their LVF. Panel adapted with permission from McGlinchey-Berroth et al. (1993). Abbreviations: AUC, area under the curve; BOLD, blood-oxygen-level-dependent; REM, rapid eye movement.

processing has already been established (Mudrik et al. 2014). Finally, neglect patients show less extinction for intact versus scrambled faces, suggesting processing without awareness (e.g., Vuilleumier 2000).

One reason for the mixed neuroimaging findings may be the use of different consciousness measures, which may substantially influence the results. This was recently demonstrated in a study where masked faces and houses were presented while measuring both graded subjective ratings of visibility and objective discrimination of a face from a house (Stein et al. 2021). Achieving objective chance-level discrimination typically requires a stronger suppression of the signal than achieving mere subjective unawareness (when subjects deny seeing the stimulus yet show above-chance discrimination), as above-chance objective performance can also be driven by unconscious processes. That was also the case in this study: chance-level discrimination involved stronger masking than subjective unawareness. Importantly, at both chance-level discrimination and subjective unawareness, objects evoked distinct category-selective activations in ventral temporal areas, suggesting that category information was present. Yet, objectively indiscriminable objects yielded less robust and less widespread activations than did subjectively unaware ones. Critically, the expected posterior-to-anterior gradient, whereby category information is better decoded in FFA or the parahippocampal place area compared to occipital areas [primary visual cortex (V1) and occipital face area or the occipital place area], was found with subjective, but not objective, criteria. These results suggest that under the stricter definition of awareness, the activation may reflect the visual (shape-related) differences between the stimuli rather than their semantics. Beyond this finding, the results also highlight the perennial conundrum around measures of awareness and how methodological choices might affect the obtained results-and the ensuing conclusions (see the sidebar titled Methodological Challenges).

There is some evidence for processing of face identity without awareness. The so-called concept neurons in the medial temporal lobe (MTL), measured by intracranial electrodes for clinical reasons, show selectivity to individual faces (Quiroga 2012). Though initial findings suggested a tight link between the spiking activity of these neurons and conscious perception (Kreiman et al. 2002), later studies implied otherwise. For example, in a recent paper using attentional blink (AB), a clear response was found for missed items in MTL single neurons (Reber et al. 2017), although

Extinction:

unawareness of contralesional stimuli that are presented together with ipsilesional stimuli, usually due to right hemisphere lesions

V1: primary visual cortex **P3:** event-related potential evoked by detection of task-relevant stimuli like a target

N2pc: an eventrelated potential component associated with spatial attention, manifested by negativity contralateral to the attended stimulus ~200 ms poststimulus presentation

Kanizsa shape:

a shape defined by illusory contours evoked by contextual inducers (e.g., three Pac-man-like figures eliciting the perception of a triangle)

Inattentional

blindness: rendering stimuli invisible (or unnoticed) due to a demanding attentional task at a different location smaller in magnitude, delayed, and more heterogenous than for seen faces (see also Quiroga et al. 2008, figure 6). With scalp EEG, self-faces and other famous faces under continuous flash suppression yielded differential activity in central electrodes between 170 and 270 ms (vertex positive potential) (Geng et al. 2012). And finally, one's own face was shown to capture spatial attention, indexed by the N2pc event-related response, even when not consciously perceived (Wójcik et al. 2019). This self-saliency is also manifested in finding a novelty P3 response to one's name, both during masking (Doradzińska et al. 2020) and during sleep (Perrin et al. 1999; for review, see Andrillon & Kouider 2020, Ibáñez et al. 2009).

Tool processing has also been widely studied, mostly addressing the hypothesis that ventral visual processing is linked to conscious perception, while dorsal activations are action-related and independent of consciousness (Milner & Goodale 1995). As tools afford action, they were surmised to activate the dorsal visual stream even without awareness. Though one study supported this dissociation, reporting preserved activations for masked tools in dorsal but not ventral areas (Fang & He 2005), some found a substantial dependency on conscious awareness in both streams (e.g., Hesselmann & Malach 2011, Ludwig et al. 2016), and others found discriminating signals to NCP tools in all four lobes (Bergström & Eriksson 2018).

Other objects may also be processed without awareness in a way that goes beyond simple object recognition. In left neglect patients, equal semantic priming was evoked by objects presented in the right and left hemifields (McGlinchey-Berroth et al. 1993) (**Figure 2**). In another, seminal work, a neglect patient was shown two line drawings of a house, where one of the houses had smoke coming from a left-side window (Marshall & Halligan 1988). Although unable to consciously detect the fire, the patient said she would prefer to live in the house that was not on fire, suggesting substantial processing. However, later attempts to replicate this finding showed that it does not occur for all tested patients, nor for all tested stimuli (Bisiach & Rusconi 1990).

All of the above studies presented stimuli in isolation, which is unnatural. Can unconscious processing also decipher objects when they appear in scenes, akin to everyday perception? One study suggested it can, when NCP man-made/natural real-life pictures of objects in scenes elicited differential activations in the right superior temporal sulcus (STS) and left parietal cortex (Fang et al. 2016). Notably though, awareness measures were taken on a separate session conducted a week later. This raises the concern that these measures might not represent the actual level of awareness of the stimuli during the main session. Conversely, another study presented NCP congruent and incongruent scenes (e.g., a woman drinking from a flower pot) and found no differential activity or decoding in any of the areas in which differential activation was found during conscious processing (Faivre et al. 2019). This null result might imply that scenes are too visually complex to be unconsciously processed, or that object-scene integration cannot be achieved without awareness, even if both are sufficiently processed, as we discuss next.

The question of the level of integration without awareness is unsettled (Moors et al. 2017, Mudrik et al. 2014, Sklar et al. 2018). Several studies suggest that some spatial integration—for example, that which is required for forming illusory contours of a Kanizsa shape (see **Figure 2a**)— is also preserved for NCP stimuli. Neglect patients show such grouping even when unaware of parts of the illusory shape (Mattingley et al. 1997, Vuilleumier et al. 2001). In healthy subjects, above-chance decoding was found for NCP Kanizsa shapes under AB (Fahrenfort et al. 2017), and differential responses were found for such shapes, compared to the control condition, in V1–V4 and in the lateral occipital complex, under inattentional blindness (IB) (Vandenbroucke et al. 2014). Since the only common feature differential activations/decoding in visual areas seems to imply that grouping indeed occurred.

LANGUAGE

Substantial research effort has been invested in unconscious language comprehension. In neglect, such processing was found for both extinguished spoken phonemes (Deouell & Soroker 2000) and words (Làdavas et al. 1993, Schweinberger & Stief 2001). For example, neglect patients presented with two different spoken syllables, simultaneously played one on each side, were only aware of hearing something on the right (i.e., displayed left extinction), yet they still reported the identity of the syllables presented on the left significantly above chance (Deouell & Soroker 2000).

In healthy subjects, word processing has typically been studied by contrasting activations evoked by words versus nonwords (or blanks), or by using a priming paradigm, where a visible target is preceded by a NCP prime, leading to repetition suppression (RS) (Larsson & Smith 2012). For example, a seminal fMRI study found that NCP masked words evoke activations ranging from extrastriate visual cortex to the visual word form area in the left fusiform gyrus (Dehaene et al. 2001). As such activations have been shown to be neural correlates of word reading (Dehaene & Cohen 2011), this suggests that word processing can take place even without awareness. Another study using masked words reported widespread activation in the left hemisphere, including the inferior frontal and the angular gyri, and posterior regions of the lateral temporal cortex, arguably parts of the neural language network (Diaz & McCarthy 2007). More recently, serially presented masked sentences elicited activations in the left posterior STS and the middle frontal gyrus compared with serially presented nonwords (Axelrod et al. 2015). Such differentiation between words and nonwords was also found in EEG under IB, starting 275–350 ms poststimulus (Ruz et al. 2005).

Do these activations represent orthographic, lexical, or semantic processes? To examine this question, one study looked for fMRI RS between Japanese Kanji and Kana scripts, which share no graphic code, and found cross-script RS in the left middle temporal gyrus (MTG), arguably reflecting post-orthographic processing (Nakamura et al. 2005) (**Figure 2**). Another study explored repetition priming between two languages (English and Japanese), reporting cross-language effects in the MTG (Nakamura et al. 2010). Using transcranial magnetic stimulation, they showed that MTG disruption decreased between-language priming. This was taken as evidence for a lexical effect rather than a semantic one, as the latter typically extends to anterolateral temporal cortex, although in previous studies MTG activation was interpreted as semantic (Nakamura et al. 2007).

Other studies argued for more advanced processing without awareness, up to the semantic level. Some relied on the activation of task-related motor areas by NCP primes (Dehaene et al. 1998, 2001). The inference of semantic effects was subsequently challenged by suggesting that these motor activations reflect consciously acquired stimulus-response contingencies (Damian 2001), rather than semantic processing. However, later studies showed that motor activations can be evoked by words even when such contingencies are avoided (for review, see Kouider & Dehaene 2007). In another paradigm, subjects falling asleep during a task requiring semantic discrimination of animal versus nonanimal names, or words versus digits, stopped pressing the right/left buttons, yet the lateralized readiness potential continued to show the semantically appropriate motor preparation during early stages of sleep (Kouider et al. 2014). Finally, successful classification of animal versus nonanimal masked words from a network of language-related areas suggested semantic processing of their content (Sheikh et al. 2019). However, this was only found when training and testing the classifier on Spanish words, as opposed to training on Spanish words and testing on Basque ones. This suggests a lexical rather than semantic effect after all. Taken together, word processing seems to occur unconsciously; clearly at the orthographic and lexical level, and possibly also semantically. Does this also mean that words can be integrated into sentences and allow for deeper-level linguistic processing?

Repetition suppression:

reduction of neural response to a repeated stimulus (of the same identity or category)

Lateralized readiness potential: an

event-related potential component indexing motor preparation, measured as the difference between left/right potentials over motor cortex

Numerous studies have shown that the amplitude of the N400 ERP is larger when a consciously perceived word is harder to interpret, because it is unexpected, rare, or novel (Kutas & Federmeier 2011). Some studies found an N400 effect to visible target words preceded by NCP incongruent versus congruent primes (Deacon et al. 2000, Holcomb et al. 2005, Kiefer 2002, Nakamura et al. 2018). However, for some of these studies, it is unclear whether subjects were completely unaware of the primes, as they were above chance in the objective measure, they were not tested at all, or unawareness was inferred from objective performance on another sample. Other studies using continuous flash suppression (CFS) or sandwich masking (for illustration of methods, see Figure 1) did not find the N400 effect (Dehaene et al. 2001, Kang et al. 2011). In these studies, the target word was consciously perceived. Only very few studies used the N400 to probe the integration of two (or more) NCP words. One found an N400 effect following a pair of a modifier and a negative/positive adjective word (e.g., "not bad") followed by an incongruent noun (e.g., "murder"), implying that the word pair could be unconsciously integrated (van Gaal et al. 2014). However, a more recent study found an N400 congruency effect for an image following a short sentence only when the sentence was not masked, whereas for single words a congruency effect was found for both masked and not masked words (Mongelli et al. 2019). Finally, an N400 effect was found for unrelated pairs of words during sleep (for review, see Ibáñez et al. 2009), though others suggested that only syllabic-level activations are evoked during sleep (see Makov et al. 2017). In one study, sentences that either included ambiguous words or not were presented to subjects while awake, lightly sedated, or strongly sedated by Propofol (Davis et al. 2007). In all conditions, differential activity between sentences and signal-correlated noise was found in the superior and middle temporal gyri. Critically, no difference was found between ambiguous and nonambiguous sentences, even at the level of light sedation.

Thus, it seems that while single words can be processed without awareness, it is still unclear to what extent such processing extends to the semantic level. Beyond single words, there is relatively little neural evidence suggesting that semantic integration can be done when the stimuli are not consciously perceived.

EMOTION

Unconscious processing of others' emotions has also been extensively studied, mostly using facial expressions. Activations evoked by NCP angry/frightened/happy/sad faces are typically compared with those evoked by NCP neutral faces. A fair amount of studies report differential activity in the amygdala (e.g., Etkin et al. 2004, Faivre et al. 2012, Killgore & Yurgelun-Todd 2004, Lapate et al. 2016, Whalen et al. 2004, Williams et al. 2006; see also Freeman et al. 2014 for an effect of facial trustworthiness), and this is supported by fMRI findings in patients with blindsight or neglect (Ajina et al. 2020, Morris et al. 2001, Vuilleumier et al. 2002a). Other structures, including the superior colliculus and locus coeruleus (Liddell et al. 2005), face-related areas like FFA and STS (e.g., Jiang & He 2006), and the inferior frontal, orbitofrontal, and anterior cingulate (Faivre et al. 2012, Nomura et al. 2004), were also differentially activated.

Another line of studies presented stimuli that were conditioned with an aversive stimulus. Right amygdala, STS, and anterior insula were activated more by masked angry faces previously paired with aversive noise or painful stimuli compared to unconditioned angry faces (Morris et al. 1998, Sabatini et al. 2009).

Emotional stimuli beyond faces have been studied, but substantially less frequently. Images of threatening animals elicited amygdala activation when they were consciously perceived but not when they were not (Hoffmann et al. 2012). NCP sexual scenes activated the reward system, among other areas, including the nucleus accumbens and the dorsal anterior cingulate cortex (Oei et al. 2012). With crowding, NCP emotional video clips elicited activation in the substantia innominata, part of the dorsal amygdaloid complex, alongside the posterior parietal cortex (PPC) (Faivre et al. 2012). With emotional words, a larger N400 component was found for emotion-incongruent target-prime trials (Kiefer et al. 2017). Beyond vision, combining fearful faces and aversive odors (both unconsciously processed) compared with neutral ones evoked activations in the right amygdala and left hippocampus, more than each modality alone (Novak et al. 2015).

However, the positive evidence described so far for processing emotion without awareness should be taken with caution. First, the findings are not consistent with respect to hemispheric involvement, finding bilateral (e.g., Dannlowski et al. 2007, Faivre et al. 2012, Williams et al. 2004), only right (e.g., Lapate et al. 2016, Vizueta et al. 2012, Yang et al. 2012), or only left (Pasley et al. 2004) activations in response to NCP emotional stimuli. Second, in some studies (Lapate et al. 2016, Pasley et al. 2004), the contrast was between emotional faces and nonfaces, so activations might simply reflect face processing. Third, the effects may subtly depend on the influence of the consciously perceived stimuli on the processing of the NCP ones; for example, one study suggested that amygdala activation is only found when the NCP face is followed by a consciously perceived face acting as a mask, and only when the eyes of the two faces spatially overlap (Straube et al. 2010). Fourth, and most importantly, in many of these studies (e.g., Killgore & Yurgelun-Todd 2004, Morris et al. 1998, Whalen et al. 1998, Williams et al. 2006), awareness was not carefully probed. For example, subjects were only asked about their awareness of the stimuli after the experiment, raising the issue of failed memory to the actual awareness experienced during the experiment; no objective measures of awareness were taken, possibly reducing the sensitivity of the measures of awareness (see the sidebar titled Methodological Challenges); or subjects were able to detect some of the faces and showed highly significant below-chance performance (rather than chance performance), leaving open the possibility that the putative evidence for processing without awareness was in fact due to trials where subjects were aware. Indeed, a recent EEG study that adopted more stringent measures of awareness than did the earlier studies in the field, with a large sample size, did not find any modulations of signals by emotional faces (Schlossmacher et al. 2017). In fMRI, some studies found amygdala activity only for consciously perceived faces (Pessoa et al. 2006, Phillips et al. 2004) or words (Hoffmann et al. 2015), and another failed to find amygdala RS for NCP emotional words, though such suppression was found in the fusiform gyrus and STS (Sabatini et al. 2009).

Thus, the disagreement around the existence and scope of unconscious processing of emotional stimuli is ongoing. If it does indeed occur, a key question is whether it depends on a quick and dirty subcortical pathway to the amygdala [e.g., via the superior colliculus and the Pulvinar (Phelps & LeDoux 2005)] or occurs via cortical pathways (Pessoa & Adolphs 2010). Regardless, much like for other types of NCP stimuli, here too bottom-up processing, rather than feedback interactions, has been suggested to subserve processing of emotional information without awareness (Freeman et al. 2014).

ATTENTION

Numerous external and internal events compete at any given moment for limited resources. Attention mechanisms bias this competition in favor of a subset of events, allocating more resources, as befits current goals (Desimone & Duncan 1995). Behaviorally, allocating attention to a stimulus generally facilitates detection and identification of attended stimuli. Since multiple neural correlates of attention allocation have been recorded with consciously perceived stimuli, these correlates can be used as an index, or a neural signature, for attention allocation to NCP stimuli. For example, akin to perceived stimuli, attention to the stimulated hand augmented

Steady-state

potential: rhythmic EEG activity evoked by rhythmically presented stimuli with the same frequency

Binocular rivalry:

presenting two different incompatible images, one to each eye, results in switches between the percepts

Exogenous attention:

attention orienting to the location of a salient, even if uninformative, cue

C1: early event-related potential, with a putative source in V1, evoked by visual stimuli ~65–90 ms poststimulus presentation

N2pc: enhanced EEG negativity over the posterior scalp contralateral, compared to ipsilateral, to the focus of attention

Endogenous

attention: top-down, goal-directed attention orienting to the location to which an informative, centrally presented cue (e.g., arrow, deviated gaze, word) was pointing somatosensory EEG evoked potentials to subthreshold electrical finger stimulation (Forschack et al. 2017), and allocating spatial attention to NCP peripheral visual gratings enhanced MEG high-frequency (75–90 Hz) response to the stimuli (Wyart & Tallon-Baudry 2008). In a well-studied effect, the amplitude of EEG steady-state potentials in response to a consciously perceived visual flicker is increased when the flickering stimulus is attended compared to not attended (Morgan et al. 1996). A similar effect of attentional enhancement of steady-state responses was found in response to NCP flickering images (Smout & Mattingley 2018).

Other attentional effects—namely, attentional load and attentional sampling—were also found to act similarly on consciously perceived and NCP stimuli. For example, peripheral, effectively masked drawings induced stronger blood-oxygen-level-dependent (BOLD) responses in early visual cortex when a central letter-detection task was easy (targets distinguished by their identity only, low load) versus hard (targets defined by a conjunction of letter and color) (Bahrami et al. 2007). As for attentional sampling, there is increasing evidence that following a cue, attention is periodically deployed to locations in the visual field at a rate of approximately 8 Hz, or 4 Hz when it switches between two locations or features (Fiebelkorn et al. 2013, Landau & Fries 2012). In an analogous way, a recent binocular rivalry study suggested that approximately 4-Hz rhythmic attentional sampling also occurs in switching between the perceived and not consciously perceived images when the switching is cued by an auditory stimulus (Davidson et al. 2018). Thus, although the literature is still limited, several neural signatures of attention allocation, previously reported for consciously perceived stimuli, have been shown to apply to NCP stimuli as well.

Another type of attentional effect in the absence of awareness pertains to exogenous attention capture: the inadvertent drawing of attentional focus by a sufficiently salient, albeit task-unrelated, stimulus. A masked, NCP array of oriented lines, some of which had a deviant orientation, exogenously captured attention to the location of the deviating lines (Zhang et al. 2012). This was manifested by an attentional facilitation of response to a subsequent consciously perceived target, which correlated with activation of V1 (fMRI) and the amplitude of the C1 ERP component. In another study, nonpredictive lateral stimuli under CFS evoked the N2pc when they shared color with the task-relevant target (Travis et al. 2019), suggesting they indeed captured attention. Furthermore, a larger N2pc was reported for NCP food items relative to nonfood items in hungry compared to not hungry subjects (Ilse et al. 2020) and to targets that were previously rewarded (Harris et al. 2016). Taken together, the data suggest that NCP stimuli may exogenously capture spatial attention and that this effect is modulated by motivational saliency.

Some have claimed that endogenous attention evoked by informative cues can also be evoked by NCP stimuli. For example, masked faces with deviated gaze yielded enhanced activations at the cued locations, in both EEG and fMRI (Chen et al. 2015, Ran et al. 2016). With the reservation that awareness was not strictly controlled in both studies, the results suggested that NCP gaze direction can cause shifts of attention. However, gaze direction is a highly learned cue for attention orienting, which may have been automatized, and relies on subcortical structures such as the superior colliculus or the amygdala, as opposed to cortical ones (Sato et al. 2016). Using more arbitrary (and arguably purely intentional) cues likely requires cortical processing, which might be more challenging without awareness. Indeed, with face gender as an endogenous cue, behavioral and electrophysiological (N1 augmentation) effects were only found for consciously perceived cues (Tipura et al. 2019). This null result may indicate either that gender is not processed without awareness (Amihai et al. 2011) or that purely endogenous, NCP cues do not direct attention (Ben-Haim et al. 2021). The latter is supported by the finding that a masked central word ("left" or "right") also did not yield the expected behavioral/electrophysiological signatures for attention shifts, although an N400 effect suggested that word meaning was processed (Baier & Ansorge 2020). Thus, endogenous attention control might indeed require awareness of the cue.

MEMORY

Data obtained from handfuls of neglect/extinction patients suggest that information about undetected stimuli may be retained over many minutes. For example, in one study, patients were presented with images of animals or artifacts at the right or left (neglected) visual field and were required to report whether they noticed the image. As expected, the patients missed most of the stimuli presented on their neglected side. Over 30 minutes later, patients were asked to recognize centrally presented blurred versions of the items from the first phase of the experiment, as well as new items. Despite missing most of the artifacts presented on the left in the first phase, patients were more accurate in recognizing these blurred artifacts (though not the animals) compared to new ones, showing that the identity of NCP items was saved nonetheless (Viggiano et al. 2012, see also Vuilleumier et al. 2002b).

In healthy subjects, unconscious sequence learning was demonstrated using dichoptic vision (Rosenthal et al. 2016). Subjects learned a high-order sequence of left- and right-hemifield circles. They were unaware of the fact that stimuli were presented independently to either the left or right eye monocularly. Nevertheless, they were more confident (though not more accurate) in recognizing old sequences in a subsequent memory test when the monocular sequence was preserved rather than altered. This advantage was correlated with fMRI activation in V1 during learning, as well as with enhanced functional connectivity between V1 and the hippocampus.

Long-term memories were also claimed to form associations between unrelated items. For example, heavily masked faces and profession names (e.g., actor, politician) that were associated during learning affected later name-profession associations, an effect that correlated with activity in the hippocampus during learning (with weak control for multiple comparisons) (Degonda et al. 2005). The same group further reported effects on episodic memory, with encoding and subsequent inference about temporal and spatial relations between objects and events. In their recent study that included an internal replication, subjects were presented with masked video clips (Schneider et al. 2021) depicting animated creatures lingering together in a hiding place. Though subjects reported not seeing the clip and were unable to say objectively which creatures hid together, they were faster in correct responses, suggesting this episodic information left a trace. Again, this effect correlated with posterior hippocampus activity (as well as other regions), yet in both studies, the control for multiple comparisons in the fMRI analysis was not strict.

Finally, working memory entails the short-term maintenance (and possible manipulation) of information in the service of an ongoing task. Since the ability to maintain information over time was claimed to be a hallmark of conscious processing (Dehaene & Naccache 2001), investigating whether unconsciously processed information may be retained over time is critical. Working memory is frequently tested with variants of the delayed match-to-sample (DMTS) task: A sample stimulus is held for a few seconds in memory, and a probe is then presented for comparison. DMTS tasks typically result in an enhanced delay BOLD signal in lateral prefrontal cortex and PPC as well as in relevant sensory cortices (Rottschy et al. 2012, Sreenivasan et al. 2014). Both the behavioral and fMRI effects were obtained even for NCP stimuli that were arguably held in memory, and the behavioral and fMRI effects were correlated both inter- and intra-individually (Dutta et al. 2014). Along the same lines, MEG data allowed quite robust decoding of the presence versus absence (and, to a substantially smaller extent, the orientation) of masked samples through a delay period (King et al. 2016).

Perhaps because working memory is intuitively associated with consciousness, studies reporting maintenance of NCP stimuli were met with criticism (Persuh et al. 2018, Stein et al. 2016). First, some claimed that consciousness was not measured stringently enough, using only subjective and not objective measures (but see Soto & Silvanto 2016). Second, recent work suggests that such effects may result from a passive mode of memory, not involving the active maintenance and manipulation of the data typical of conscious processing. Arguably, once manipulation of the memoranda is required (e.g., mental rotation), subjects engage in an active working memory process performed on a conscious guess (Trubutschek et al. 2019). Thus, this question also requires further research.

CONCLUSIONS

This review encompasses many reports of neural responses to NCP stimuli, implying different types of information processing without awareness. By and large, the responses are weaker and noisier than for consciously perceived stimuli. This potentially quantitative difference between conscious and unconscious processes could be partly because of the methods required to render stimuli imperceptible, which require some deterioration of the stimuli. Alternatively, it could reflect the amplification of signal afforded by conscious processing (Dehaene et al. 2006). Yet some studies suggest that the two types of processes might also qualitatively differ: For example, while suprathreshold stimulation suppresses alpha power, subthreshold low-contrast stimuli enhanced alpha power and impaired the perception of consciously perceived targets, suggesting cortical inhibition rather than activation (Bareither et al. 2014). Thus, more research is needed to fully expose the qualitative and quantitative difference between processing of consciously and unconsciously perceived stimuli. Irrespective of this question, though, and notwithstanding the null findings that are also frequently observed, some positive conclusions can be made. First, there is a substantial amount of evidence for sensitive and discriminatory neural responses to some high-level perceptual information, linguistic material, and emotion. Second, these responses seem to interact with attention and memory. Third, the data are scanter and more conflicting regarding the highest level of integration of scenes or multiword phrases.

As we repeatedly emphasized above, evidence for processing without awareness heavily depends on convincingly demonstrating that subjects were indeed unaware of the stimuli. The studies reviewed here differ regarding whether (un)awareness was measured based on subjective report or by objective performance. The former may be too liberal if observers report no visibility when they still have partial awareness. The latter may be too conservative, as above-chance objective performance might stem from unconscious processing (see the sidebar titled Methodological Challenges). Undoubtedly, results are influenced by this conceptual, not only methodological, choice (Stein et al. 2021). A more serious concern is the quality and reliability of these measures, which are sometimes not administered with enough rigor (e.g., using binary subjective measures, not testing on a trial-by-trial basis, having too few trials in the objective measure, or conducting the objective test under different conditions). This leaves open the possibility that some of the neural effects are driven by occasional trials in which subjects were conscious of the stimuli. As the field moves forward, more stringent policies are being adopted, which will allow more reliable interpretations of the neural results (Rothkirch & Hesselmann 2017).

Another source of variability between studies may be individual differences in susceptibility to subliminal information, either as trait or as state. For example, responses to NCP emotional faces correlate with the trait of negative affectivity (Etkin et al. 2004, Vizueta et al. 2012), unconscious memory effects were only found in subjects leaning toward an intuitive decision-making style (Schneider et al. 2021), and subliminal food images captured attention in hungry but not in satiated subjects (Ilse et al. 2020). This is an important avenue for future research.

To conclude, this review describes a wide array of processing types and methods showing that a specific function can be performed—to some extent—without awareness. Do they all combine into a coherent neuroscientific account of processing without awareness? The honest answer is no. The field is lacking larger-scale studies, including different types of processes and directly

Mudrik • Deouell

assessing the contribution of conscious versus unconscious processing to performance. Only such studies will be able to shed light on the truly interesting questions: to what extent the processing of NCP input affects behavior, and how conscious and unconscious processes interact.

SUMMARY POINTS

- 1. Neural signatures of processing, and decoding of stimulus information from neural signals, complement behavior in assessing the extent of processing evoked by not consciously perceived (NCP) stimuli.
- 2. Establishing processing of NCP stimuli requires care, both in analyzing weak brain signals and in ensuring lack of conscious awareness.
- 3. Despite methodological criticism and sometimes conflicting findings, evidence largely suggests processing of low-level and some high-level information, including object categories (faces, tools) and words.
- 4. Evidence for integration of more than two words into sentences or scenes with objects is scant.
- 5. Processing of NCP objects is enhanced by attention allocation.
- 6. NCP stimuli orient attention exogenously, but evidence for endogenous orienting is lacking.
- 7. NCP stimuli may be retained in long-term memory and to some extent in working memory.

FUTURE ISSUES

- 1. Improved computational tools for decoding/encoding information from brain signals coupled with stimulation tools for perturbation can be a powerful method for assessing the processing of not consciously perceived stimuli.
- 2. Large-scale studies testing multiple levels and domains of processing in the same subjects are needed to better chart the extent of processing and its generalizability.
- 3. Individual differences in processing of not consciously perceived information should be extensively explored to explain variability in results.
- 4. The lessons learned from the replicability crisis should be applied to improve the credibility of the results in this contentious field.

DISCLOSURE STATEMENT

L.Y.D. is the co-founder and Chief Science Officer of Innereye Ltd., a startup company in the field of neurotechnology. L.M. is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We deeply thank Shai Fischer, Rotem Krispil, Yael Solar Priel, and Karin Uritsky for their extensive work on gathering and analyzing the reviewed papers. L.M. is supported by the Human

Frontier Science Program (CDA00061-2018) and is a CIFAR Tanenbaum Fellow in the Brain, Mind & Consciousness program. L.Y.D. is supported by the Jack H. Skirball research fund and by the Israel Science Foundation Bikura Fund (grant number 3504/20).

LITERATURE CITED

- Ajina S, Pollard M, Bridge H. 2020. The superior colliculus and amygdala support evaluation of face trait in blindsight. *Front. Neurol.* 11:769
- Amihai I, Deouell L, Bentin S. 2011. Conscious awareness is necessary for processing race and gender information from faces. Conscious. Cogn. 20(2):269–79
- Andrillon T, Kouider S. 2020. The vigilant sleeper: neural mechanisms of sensory (de)coupling during sleep. *Curr. Opin. Physiol.* 15:47–59
- Axelrod V, Bar M, Rees G, Yovel G. 2015. Neural correlates of subliminal language processing. Cereb. Cortex 25(8):2160–69
- Bahrami B, Lavie N, Rees G. 2007. Attentional load modulates responses of human primary visual cortex to invisible stimuli. Curr. Biol. 17(6):509–13
- Baier D, Ansorge U. 2020. Can subliminal spatial words trigger an attention shift? Evidence from eventrelated-potentials in visual cueing. Vis. Cogn. 28(1):10–32
- Bareither I, Chaumon M, Bernasconi F, Villringer A, Busch NA. 2014. Invisible visual stimuli elicit increases in alpha-band power. J. Neurophysiol. 112(5):1082–90
- Ben-Haim MS, Dal Monte O, Fagan NA, Dunham Y, Hassin RR, et al. 2021. Disentangling perceptual awareness from nonconscious processing in rhesus monkeys (*Macaca mulatta*). PNAS 118(15):e2017543118
- Bentin S, Allison T, Puce A, Perez E, McCarthy G. 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8(6):551–65
- Bergström F, Eriksson J. 2018. Neural evidence for non-conscious working memory. Cereb. Cortex 28(9):3217– 28
- Bisiach E, Rusconi ML. 1990. Break-down of perceptual awareness in unilateral neglect. Cortex 26(4):643-49
- Breitmeyer BG. 2015. Psychophysical "blinding" methods reveal a functional hierarchy of unconscious visual processing. Conscious. Cogn. 35:234–50
- Chen X, Ran G, Zhang Q, Hu T. 2015. Unconscious attention modulates the silencing effect of top-down predictions. *Conscious. Cogn.* 34:63–72
- Damian MF. 2001. Congruity effects evoked by subliminally presented primes: automaticity rather than semantic processing. J. Exp. Psychol. Hum. Percept. Perform. 27(1):154–65
- Dannlowski U, Ohrmann P, Bauer J, Kugel H, Arolt V, et al. 2007. Amygdala reactivity predicts automatic negative evaluations for facial emotions. *Psychiatry Res.* 154(1):13–20
- Davidson MJ, Alais D, van Boxtel JJA, Tsuchiya N. 2018. Attention periodically samples competing stimuli during binocular rivalry. *eLife* 7:e40868
- Davis MH, Coleman MR, Absalom AR, Rodd JM, Johnsrude IS, et al. 2007. Dissociating speech perception and comprehension at reduced levels of awareness. PNAS 104(41):16032–37
- Deacon D, Hewitt S, Yang CM, Nagata M. 2000. Event-related potential indices of semantic priming using masked and unmasked words: evidence that the N400 does not reflect a post-lexical process. *Cogn. Brain Res.* 9(2):137–46
- Degonda N, Mondadori CRA, Bosshardt S, Schmidt CF, Boesiger P, et al. 2005. Implicit associative learning engages the hippocampus and interacts with explicit associative learning. *Neuron* 46(3):505–20
- Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C. 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10(5):204–11
- Dehaene S, Cohen L. 2011. The unique role of the visual word form area in reading. *Trends Cogn. Sci.* 15(6):254-62
- Dehaene S, Naccache L. 2001. Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79(1–2):1–37
- Dehaene S, Naccache L, Cohen L, Le Bihan D, Mangin JF, et al. 2001. Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4:752–58

- Dehaene S, Naccache L, Le Clec'H G, Koechlin E, Mueller M, et al. 1998. Imaging unconscious semantic priming. Nature 395(6702):597–600
- Deouell LY, Soroker N. 2000. What is extinguished in auditory extinction? Neuroreport 11(13):3059-62
- Desimone R, Duncan J. 1995. Neural mechanisms of selective visual-attention. Annu. Rev. Neurosci. 18:193–222
- Diaz MT, McCarthy G. 2007. Unconscious word processing engages a distributed network of brain regions. J. Cogn. Neurosci. 19(11):1768–75
- Doradzińska Ł, Wójcik MJ, Paź M, Nowicka MM, Nowicka A, Bola M. 2020. Unconscious perception of one's own name modulates amplitude of the P3B ERP component. *Neuropsychologia* 147:107564
- Dutta A, Shah K, Silvanto J, Soto D. 2014. Neural basis of non-conscious visual working memory. *Neuroimage* 91:336–43
- Etkin A, Klemenhagen KC, Dudman JT, Rogan MT, Hen R, et al. 2004. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. *Neuron* 44(6):1043–55
- Fahrenfort JJ, Snijders TM, Heinen K, Van Gaal S, Scholte HS, Lamme VAF. 2012. Neuronal integration in visual cortex elevates face category tuning to conscious face perception. PNAS 109(52):21504–509
- Fahrenfort JJ, van Leeuwen J, Olivers CNL, Hogendoorn H. 2017. Perceptual integration without conscious access. PNAS 114(14):3744–49
- Faivre N, Charron S, Roux P, Lehéricy S, Kouide S. 2012. Nonconscious emotional processing involves distinct neural pathways for pictures and videos. *Neuropsychologia* 50(14):3736–44
- Faivre N, Dubois J, Schwartz N, Mudrik L. 2019. Imaging object-scene relations processing in visible and invisible natural scenes. Sci. Rep. 9(1):4567
- Fang F, He S. 2005. Cortical responses to invisible objects in the human dorsal and ventral pathways. Nat. Neurosci. 8(10):1380–85
- Fang Z, Li H, Chen G, Yang J. 2016. Unconscious processing of negative animals and objects: role of the amygdala revealed by fMRI. *Front. Hum. Neurosci.* 10:146
- Fiebelkorn IC, Saalmann YB, Kastner S. 2013. Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr. Biol.* 23:2553–58
- Forschack N, Nierhaus T, Müller MM, Villringer A. 2017. Alpha-band brain oscillations shape the processing of perceptible as well as imperceptible somatosensory stimuli during selective attention. *J. Neurosci.* 37(29):6983–94
- Forschack N, Nierhaus T, Müller MM, Villringer A. 2020. Dissociable neural correlates of stimulation intensity and detection in somatosensation. *Neuroimage* 217:116908
- Freeman JB, Stolier RM, Ingbretsen ZA, Hehman EA. 2014. Amygdala responsivity to high-level social information from unseen faces. J. Neurosci. 34(32):10573–581
- Freud S. 2005. The Unconscious. London: Penguin
- Ganesh G, Nakamura K, Saetia S, Tobar AM, Yoshida E, et al. 2018. Utilizing sensory prediction errors for movement intention decoding: a new methodology. Sci. Adv. 4(5):eaaq0183
- Geng H, Zhang S, Li Q, Tao R, Xu S. 2012. Dissociations of subliminal and supraliminal self-face from other-face processing: behavioral and ERP evidence. *Neuropsychologia* 50(12):2933–42
- Harris JA, Donohue SE, Schoenfeld MA, Hopf J-M, Heinze H-J, Woldorff MG. 2016. Reward-associated features capture attention in the absence of awareness: evidence from object-substitution masking. *Neuroimage* 137:116–23
- Harris JA, McMahon AR, Woldorff MG. 2013. Disruption of visual awareness during the attentional blink is reflected by selective disruption of late-stage neural processing. *J. Cogn. Neurosci.* 25(11):1863–74
- Haxby JV, Hoffman EA, Gobbini MI. 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4(6):223–33
- Hesselmann G, Malach R. 2011. The link between fMRI-BOLD activation and perceptual awareness is "stream-invariant" in the human visual system. *Cereb. Cortex* 21(12):2829–37
- Hoffmann M, Lipka J, Mothes-Lasch M, Miltner WHR, Straube T. 2012. Awareness modulates responses of the amygdala and the visual cortex to highly arousing visual threat. *Neuroimage* 62(3):1439–44
- Hoffmann M, Mothes-Lasch M, Miltner WHR, Straube T. 2015. Brain activation to briefly presented emotional words: effects of stimulus awareness. *Hum. Brain Mapp.* 36(2):655–65

- Holcomb PJ, Reder L, Misra M, Grainger J. 2005. The effects of prime visibility on ERP measures of masked priming. Cogn. Brain Res. 24(1):155–72
- Ibáñez AM, Martín RS, Hurtado E, López V. 2009. ERPs studies of cognitive processing during sleep. Int. J. Psychol. 44(4):290–304
- Ilse A, Donohue SE, Schoenfeld MA, Hopf JM, Heinze HJ, Harris JA. 2020. Unseen food images capture the attention of hungry viewers: evidence from event-related potentials. *Appetite* 155:104828
- Jiang Y, He S. 2006. Cortical responses to invisible faces: dissociating subsystems for facial-information processing. Curr. Biol. 16(20):2023–29
- Kang MS, Blake R, Woodman GF. 2011. Semantic analysis does not occur in the absence of awareness induced by interocular suppression. J. Neurosci. 31(38):13535–45
- Kiefer M. 2002. The N400 is modulated by unconsciously perceived masked words: further evidence for an automatic spreading activation account of N400 priming effects. *Cogn. Brain Res.* 13(1):27–39
- Kiefer M, Liegel N, Zovko M, Wentura D. 2017. Mechanisms of masked evaluative priming: task sets modulate behavioral and electrophysiological priming for picture and words differentially. Soc. Cogn. Affect. Neurosci. 12(4):596–608
- Killgore WDS, Yurgelun-Todd DA. 2004. Activation of the amygdala and anterior cingulate during nonconscious processing of sad versus happy faces. *Neuroimage* 21(4):1215–23
- Kim CY, Blake R. 2005. Psychophysical magic: rendering the visible 'invisible'. Trends Cogn. Sci. 9(8):381-88
- King JR, Pescetelli N, Dehaene S. 2016. Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron* 92(5):1122–34
- Kouider S, Andrillon T, Barbosa LS, Goupil L, Bekinschtein TA. 2014. Inducing task-relevant responses to speech in the sleeping brain. Curr. Biol. 24(18):2208–14
- Kouider S, Dehaene S. 2007. Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. B* 362(1481):857–75
- Kouider S, Eger E, Dolan R, Henson RN. 2009. Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cereb. Cortex* 19(1):13–23
- Kreiman G, Fried I, Koch C. 2002. Single-neuron correlates of subjective vision in the human medial temporal lobe. PNAS 99(12):8378–83
- Kutas M, Federmeier KD. 2011. Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). Annu. Rev. Psychol. 62:621–47
- Làdavas E, Paladini R, Cubelli R. 1993. Implicit associative priming in a patient with left visual neglect. Neuropsychologia 31(12):1307–20
- Lamme VAF. 2020. Visual functions generating conscious seeing. Front. Psychol. 11:83
- Landau AN, Fries P. 2012. Attention samples stimuli rhythmically. Curr. Biol. 22(11):1000-4
- Lapate RC, Rokers B, Tromp DPM, Orfali NS, Oler JA, et al. 2016. Awareness of emotional stimuli determines the behavioral consequences of amygdala activation and amygdala-prefrontal connectivity. Sci. Rep. 6(1):25826
- Larsson J, Smith AT. 2012. fMRI repetition suppression: neuronal adaptation or stimulus expectation? Cereb. Cortex 22(3):567–76
- Liddell BJ, Brown KJ, Kemp AH, Barton MJ, Das P, et al. 2005. A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *Neuroimage* 24(1):235–43
- Ludwig K, Sterzer P, Kathmann N, Hesselmann G. 2016. Differential modulation of visual object processing in dorsal and ventral stream by stimulus visibility. *Cortex* 83:113–23
- Makov S, Sharon O, Ding N, Ben-Shachar M, Nir Y, Golumbic Zion E. 2017. Sleep disrupts high-level speech parsing despite significant basic auditory processing. J. Neurosci. 37(32):7772–81
- Maresch J, Mudrik L, Donchin O. 2021. Measures of explicit and implicit in motor learning: what we know and what we don't. *Neurosci. Biobehav. Rev.* 128:558–68
- Marshall JC, Halligan PW. 1988. Blindsight and insight in visuo-spatial neglect. Nature 336(6201):766-67
- Mattingley JB, Davis G, Driver J. 1997. Preattentive filling-in of visual surfaces in parietal extinction. Science 275(5300):671–74
- McGlinchey-Berroth R, Milberg WP, Verfaellie M, Alexander M, Kilduff PT. 1993. Semantic processing in the neglected visual field: evidence from a lexical decision task. *Cogn. Neuropsychol.* 10(1):79–108

- Merikle P, Reingold E. 1998. On demonstrating unconscious perception: comment on Draine and Greenwald (1998). 7. Exp. Psychol. Gen. 127(3):304–10
- Milner AD, Goodale MA. 1995. The Visual Brain in Action. New York: Oxford Univ. Press
- Mongelli V, Meijs EL, Van Gaal S, Hagoort P. 2019. No language unification without neural feedback: how awareness affects sentence processing. *Neuroimage* 202:116063
- Moors P, Hesselmann G, Wagemans J, van Ee R. 2017. Continuous flash suppression: stimulus fractionation rather than integration. *Trends Cogn. Sci.* 21:719–21
- Morgan ST, Hansen JC, Hillyard SA. 1996. Selective attention to stimulus location modulates the steady-state visual evoked potential. PNAS 93(10):4770–74
- Morris JS, DeGelder B, Weiskrantz L, Dolan RJ. 2001. Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain* 124(6):1241–52
- Morris JS, Ohman A, Dolan RJ. 1998. Conscious and unconscious emotional learning in the human amygdala. *Nature* 393(6684):467–70
- Moutoussis K, Zeki S. 2006. Seeing invisible motion: a human fMRI study. Curr. Biol. 16(6):574-79
- Mudrik L, Faivre N, Koch C. 2014. Information integration without awareness. Trends Cogn. Sci. 18(9):488-96
- Nakamura K, Dehaene S, Jobert A, Le Bihan D, Kouider S. 2005. Subliminal convergence of Kanji and Kana words: further evidence for functional parcellation of the posterior temporal cortex in visual word perception. *J. Cogn. Neurosci.* 17(6):954–68
- Nakamura K, Dehaene S, Jobert A, Le Bihan D, Kouider S. 2007. Task-specific change of unconscious neural priming in the cerebral language network. PNAS 104(49):19643–48
- Nakamura K, Kouider S, Makuuchi M, Kuroki C, Hanajima R, et al. 2010. Neural control of cross-language asymmetry in the bilingual brain. Cereb. Cortex 20(9):2244–51
- Nakamura K, Makuuchi M, Oga T, Mizuochi-Endo T, Iwabuchi T, et al. 2018. Neural capacity limits during unconscious semantic processing. *Eur. J. Neurosci.* 47(8):929–37
- Nomura M, Ohira H, Haneda K, Iidaka T, Sadato N, et al. 2004. Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: an event-related fMRI study. *Neuroimage* 21(1):352–63
- Novak LR, Gitelman DR, Schuyler B, Li W. 2015. Olfactory-visual integration facilitates perception of subthreshold negative emotion. *Neuropsychologia* 77:288–97
- Oei NYL, Arb Rombouts S, Soeter RP, Van Gerven JM, Both S. 2012. Dopamine modulates reward system activity during subconscious processing of sexual stimuli. *Neuropsychopharmacology* 37(7):1729–37
- Pasley BN, Mayes LC, Schultz RT. 2004. Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42(1):163–72
- Perrin F, Garciá-Larrea L, Mauguière F, Bastuji H. 1999. A differential brain response to the subject's own name persists during sleep. *Clin. Neurophysiol.* 110(12):2153–64
- Persuh M, LaRock E, Berger J. 2018. Working memory and consciousness: the current state of play. *Front. Hum. Neurosci.* 12:78
- Pessoa L, Adolphs R. 2010. Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nat. Rev. Neurosci.* 11(11):773–82
- Pessoa L, Japee S, Sturman D, Ungerleider LG. 2006. Target visibility and visual awareness modulate amygdala responses to fearful faces. *Cereb. Cortex* 16(3):366–75
- Phelps EA, LeDoux JE. 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron* 48(2):175–87
- Phillips ML, Williams LM, Heining M, Herba CM, Russell T, et al. 2004. Differential neural responses to overt and covert presentations of facial expressions of fear and disgust. *Neuroimage* 21(4):1484–96
- Pitts MA, Martínez A, Hillyard SA. 2012. Visual processing of contour patterns under conditions of inattentional blindness. J. Cogn. Neurosci. 24(2):287–303
- Pitts MA, Padwal J, Fennelly D, Martínez A, Hillyard SA. 2014. Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *Neuroimage* 101:337–50
- Poldrack RA. 2006. Can cognitive processes be inferred from neuroimaging data? Trends Cogn. Sci. 10(2):59-63
- Quiroga RQ. 2012. Concept cells: the building blocks of declarative memory functions. Nat. Rev. Neurosci. 13(8):587–97

- Quiroga RQ, Mukamel R, Isham EA, Malach R, Fried I. 2008. Human single-neuron responses at the threshold of conscious recognition. PNAS 105(9):3599–604
- Ran G, Chen X, Cao X, Zhang Q. 2016. Prediction and unconscious attention operate synergistically to facilitate stimulus processing: an fMRI study. *Conscious. Cogn.* 44:41–50
- Reber TP, Faber J, Niediek J, Boström J, Elger CE, Mormann F. 2017. Single-neuron correlates of conscious perception in the human medial temporal lobe. *Curr. Biol.* 27(19):2991–98.e2
- Rodríguez V, Thompson R, Stokes M, Brett M, Alvarez I, et al. 2012. Absence of face-specific cortical activity in the complete absence of awareness: converging evidence from functional magnetic resonance imaging and event-related potentials. *J. Cogn. Neurosci.* 24(2):396–415
- Rosenthal CR., Andrews SK, Antoniades CA, Kennard C, Soto D. 2016. Learning and recognition of a non-conscious sequence of events in human primary visual cortex. *Curr. Biol.* 26(6):834–41
- Rothkirch M, Hesselmann G. 2017. What we talk about when we talk about unconscious processing—a plea for best practices. *Front. Psychol.* 8:835
- Rottschy C, Langner R, Dogan I, Reetz K, Laird AR, et al. 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. *Neuroimage* 60(1):830–46
- Ruz M, Worden MS, Tudela P, McCandliss BD. 2005. Inattentional amnesia to words in a high attentional load task. J. Cogn. Neurosci. 17(5):768–76
- Sabatini E, Della Penna S, Franciotti R, Ferretti A, Zoccolotti P, et al. 2009. Brain structures activated by overt and covert emotional visual stimuli. *Brain Res. Bull.* 79(5):258–64
- Sandberg K, Timmermans B, Overgaard M, Cleeremans A. 2010. Measuring consciousness: Is one measure better than the other? *Conscious. Cogn.* (19):1069–78
- Sato W, Kochiyama T, Uono S, Toichi M. 2016. Neural mechanisms underlying conscious and unconscious attentional shifts triggered by eye gaze. *Neuroimage* 124:118–26
- Schelling FWJ. 1993. System of Transcendental Idealism (1800). Charlottesville, VA: Univ. Va. Press
- Schlossmacher I, Junghöfer M, Straube T, Bruchmann M. 2017. No differential effects to facial expressions under continuous flash suppression: an event-related potentials study. *Neuroimage* 163:276–85
- Schneider E, Züst MA, Wuethrich S, Schmidig F, Klöppel S, et al. 2021. Larger capacity for unconscious versus conscious episodic memory. *Curr. Biol.* 31(16):3551–63.e9
- Schweinberger SR, Stief V. 2001. Implicit perception in patients with visual neglect: lexical specificity in repetition priming. *Neuropsychologia* 39(4):420–29
- Sculthorpe LD, Ouellet DR, Campbell KB. 2009. MMN elicitation during natural sleep to violations of an auditory pattern. *Brain Res.* 1290:52–62
- Shafto JP, Pitts MA. 2015. Neural signatures of conscious face perception in an inattentional blindness paradigm. J. Neurosci. 35(31):10940–48
- Shanks DR. 2017. Regressive research: the pitfalls of post hoc data selection in the study of unconscious mental processes. *Psychon. Bull. Rev.* 24:752–75
- Sheikh UA, Carreiras M, Soto D. 2019. Decoding the meaning of unconsciously processed words using fMRIbased MVPA. Neuroimage 191:430–40
- Sklar A, Deouell LY, Hassin R. 2018. Integration despite fractionation: continuous flash suppression. Trends Cogn. Sci. 22:956–57
- Smout CA, Mattingley JB. 2018. Spatial attention enhances the neural representation of invisible signals embedded in noise. *J. Cogn. Neurosci.* 30(8):1119–29
- Soto D, Silvanto J. 2016. Is conscious awareness needed for all working memory processes? *Neurosci. Conscious*. 2016:niw009
- Sreenivasan KK, Curtis CE, D'Esposito M. 2014. Revisiting the role of persistent neural activity during working memory. *Trends Cogn. Sci.* 18(2):82–89
- Stein T, Kaiser D, Fahrenfort JJ, Van Gaal S. 2021. The human visual system differentially represents subjectively and objectively invisible stimuli. PLOS Biol. 19(5):e3001241
- Stein T, Kaiser D, Hesselmann G. 2016. Can working memory be non-conscious? Neurosci. Conscious. 2016:niv011
- Sterzer P, Jalkanen L, Rees G. 2009. Electromagnetic responses to invisible face stimuli during binocular suppression. *Neuroimage* 46(3):803–8

- Straube T, Dietrich C, Mothes-Lasch M, Mentzel HJ, Miltner WHR. 2010. The volatility of the amygdala response to masked fearful eyes. *Hum. Brain Mapp.* 31(10):1601–8
- Suzuki M, Noguchi Y. 2013. Reversal of the face-inversion effect in N170 under unconscious visual processing. *Neuropsychologia* 51(3):400–9
- Suzuki M, Noguchi Y, Kakigi R. 2014. Temporal dynamics of neural activity underlying unconscious processing of manipulable objects. *Cortex* 50:100–14
- Tettamanti M, Conca F, Falini A, Perani D. 2017. Unaware processing of tools in the neural system for objectdirected action representation. *J. Neurosci.* 37(44):10712–24
- Tipura E, Renaud O, Pegna AJ. 2019. Attention shifting and subliminal cueing under high attentional load: an EEG study using emotional faces. *Neuroreport* 30(18):1251–55
- Travis SL, Dux PE, Mattingley JB. 2019. Neural correlates of goal-directed enhancement and suppression of visual stimuli in the absence of conscious perception. *Attention Percept. Psychophys.* 81(5):1346–64
- Trubutschek D, Marti S, Ueberschar H, Dehaene S. 2019. Probing the limits of activity-silent non-conscious working memory. PNAS 116(28):14358–67
- van Gaal S, Naccache L, Meuwese JD, van Loon AM, Leighton AH, et al. 2014. Can the meaning of multiple words be integrated unconsciously? *Philos. Trans. R. Soc. B* 369(1641):20130212
- Vandenbroucke ARE, Fahrenfort JJ, Sligte IG, Lamme VAF. 2014. Seeing without knowing: neural signatures of perceptual inference in the absence of report. J. Cogn. Neurosci. 26(5):955–69
- Viggiano MP, Marzi T, Forni M, Righi S, Franceschini R, Peru A. 2012. Semantic category effects modulate visual priming in neglect patients. *Cortex* 48(9):1128–37
- Vizueta N, Patrick CJ, Jiang Y, Thomas KM, He S. 2012. Dispositional fear, negative affectivity, and neuroimaging response to visually suppressed emotional faces. *Neuroimage* 59(1):761–71
- Vuilleumier P. 2000. Faces call for attention: evidence from patients with visual extinction. Neuropsychologia 38(5):693–700
- Vuilleumier P, Armony JL, Clarke K, Husain M, Driver J, Dolan RJ. 2002a. Neural response to emotional faces with and without awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia* 40(12):2156–66
- Vuilleumier P, Schwartz S, Clarke K, Husain M, Driver J. 2002b. Testing memory for unseen visual stimuli in patients with extinction and spatial neglect. J. Cogn. Neurosci. 14(6):875–86
- Vuilleumier P, Valenza N, Landis T. 2001. Explicit and implicit perception of illusory contours in unilateral spatial neglect: behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia* 39(6):597–10
- Whalen PJ, Kagan J, Cook RG, Davis FC, Kim H, et al. 2004. Human amygdala responsivity to masked fearful eye whites. Science 306(5704):2061–61
- Whalen PJ, Rauch SL, Etcoff NL, McInerney SC, Lee MB, Jenike MA. 1998. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. J. Neurosci. 18(1):411–18
- Williams LM, Das P, Liddell BJ, Kemp AH, Rennie CJ, Gordon E. 2006. Mode of functional connectivity in amygdala pathways dissociates level of awareness for signals of fear. J. Neurosci. 26(36):9264–71
- Williams MA, Morris AP, McGlone F, Abbott DF, Mattingley JB. 2004. Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. J. Neurosci. 24(12):2898–904
- Wójcik MJ, Nowicka MM, Bola M, Nowicka A. 2019. Unconscious detection of one's own image. Psychol. Sci. 30(4):471–80
- Wyart V, Tallon-Baudry C. 2008. Neural dissociation between visual awareness and spatial attention. J. Neurosci. 28(10):2667–79
- Yang J, Cao Z, Xu X, Chen G. 2012. The amygdala is involved in affective priming effect for fearful faces. Brain Cogn. 80(1):15–22
- Zhang X, Zhaoping L, Zhou T, Fang F. 2012. Neural activities in V1 create a bottom-up saliency map. *Neuron* 73(1):183–92
- Zou J, He S, Zhang P. 2016. Binocular rivalry from invisible patterns. PNAS 113(30):8408-13



Annual Review of Neuroscience

Volume 45, 2022

Contents

Multiple-Timescale Representations of Space: Linking Memory to Navigation <i>Wenbo Tang and Shantanu P. Jadhav</i>
Challenges of Organoid Research Madeline G. Andrews and Arnold R. Kriegstein
Receptor-Ribosome Coupling: A Link Between Extrinsic Signals and mRNA Translation in Neuronal Compartments <i>Max Koppers and Christine E. Holt</i>
Brainstem Circuits for Locomotion Roberto Leiras, Jared M. Cregg, and Ole Kiehn
Signaling Pathways in Neurovascular Development Amir Rattner, Yanshu Wang, and Jeremy Nathans
Mesoaccumbal Dopamine Heterogeneity: What Do Dopamine Firing and Release Have to Do with It? <i>Johannes W. de Jong, Kurt M. Fraser, and Stephan Lammel</i>
Melding Synthetic Molecules and Genetically Encoded Proteins to Forge New Tools for Neuroscience <i>Pratik Kumar and Luke D. Lavis</i>
The Cerebellar Cortex Court Hull and Wade G. Regebr
Clearing Your Mind: Mechanisms of Debris Clearance After Cell Death During Neural Development <i>Kendra E. Liu, Michael H. Raymond, Kodi S. Ravichandran, and Sarah Kucenas</i> 177
Neural Signaling in Cancer Michael B. Keough and Michelle Monje
Breathing Rhythm and Pattern and Their Influence on Emotion Sufyan Ashhad, Kaiwen Kam, Christopher A. Del Negro, and Jack L. Feldman 223
Neural Algorithms and Circuits for Motor Planning Hidebiko K. Inagaki, Susu Chen, Kayvon Daie, Arseny Finkelstein, Lorenzo Fontolan, Sandro Romani, and Karel Svoboda

 Fluorescence Imaging of Neural Activity, Neurochemical Dynamics, and Drug-Specific Receptor Conformation with Genetically Encoded Sensors <i>Chunyang Dong, Yu Zheng, Kiran Long-Iyer, Emily C. Wright, Yulong Li,</i> and Lin Tian
A Theoretical Framework for Human and Nonhuman Vocal Interaction Gregg A. Castellucci, Frank H. Guenther, and Michael A. Long
Neuromodulation and Neurophysiology on the Timescale of Learning and Decision-Making <i>Cooper D. Grossman and Jeremiab Y. Cohen</i>
Neuroimmune Interactions in Peripheral Organs Roel G.J. Klein Wolterink, Glendon S. Wu, Isaac M. Chiu, and Henrique Veiga-Fernandes
Subcortical Cognition: The Fruit Below the Rind Karolina Janacsek, Tanya M. Evans, Mariann Kiss, Leela Shah, Hal Blumenfeld, and Michael T. Ullman
Considering Organismal Physiology in Laboratory Studies of Rodent Behavior Patricia Rubio Arzola and Rebecca M. Shansky
Neuroscientific Evidence for Processing Without Awareness Liad Mudrik and Leon Y. Deouell
Microglia and Neurodevelopmental Disorders John R. Lukens and Ukpong B. Eyo
 Adeno-Associated Virus Toolkit to Target Diverse Brain Cells Rosemary C. Challis, Sripriya Ravindra Kumar, Xinhong Chen, David Goertsen, Gerard M. Coughlin, Acacia M. Hori, Miguel R. Chuapoco, Thomas S. Otis, Timothy F. Miles, and Viviana Gradinaru
Cross-Modal Plasticity in Brains Deprived of Visual Input Before Vision <i>Guillermina López-Bendito, Mar Aníbal-Martínez, and Francisco J. Martini</i>
Functional Ultrasound Neuroimaging Gabriel Montaldo, Alan Urban, and Emilie Macé
Human Cerebellar Development and Transcriptomics: Implications for Neurodevelopmental Disorders <i>Parthiv Haldipur, Kathleen J. Millen, and Kimberly A. Aldinger</i>

Theory of the Multiregional Neocortex: Large-Scale Neural
Dynamics and Distributed Cognition
Xiao-Jing Wang
Beyond Wrapping: Canonical and Noncanonical Functions of
Schwann Cells
Carla Taveggia and M. Laura Feltri
Synaptic Mechanisms Regulating Mood State Transitions
in Depression
Puja K. Parekh, Shane B. Johnson, and Conor Liston

Indexes

Cumulative Index of Contributing Authors, Volu	imes 36–45 603
--	----------------

Errata

An online log of corrections to *Annual Review of Neuroscience* articles may be found at http://www.annualreviews.org/errata/neuro