Review

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Information integration without awareness

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Information integration and consciousness are closely related, if not interdependent. But, what exactly is the nature of their relation? Which forms of integration require consciousness? Here, we examine the recent experimental literature with respect to perceptual and cognitive integration of spatiotemporal, multisensory, semantic, and novel information. We suggest that, whereas some integrative processes can occur without awareness, their scope is limited to smaller integration windows, to simpler associations, or to ones that were previously acquired consciously. This challenges previous claims that consciousness of some content is necessary for its integration; yet it also suggests that consciousness holds an enabling role in establishing integrative mechanisms that can later operate unconsciously, and in allowing wider-range integration, over bigger semantic, spatiotemporal, and sensory integration windows.

Integration and consciousness: a redefinition of their possible relations

In the scientific study of consciousness, great emphasis is placed on integration (defined further below): it is held to go hand in hand with consciousness, reflecting both the unified and holistic nature of conscious experience and the hypothesis that consciousness is needed for integration to occur (see Table 1 for quotes from influential publications in the field). Traces for this potential close tie date back at least to the writings of Descartes [1], Kant [2], or James [3] (Table 1). This long tradition of coupling consciousness with integration has a strong influence on current thinking. In this review, the main statements relating consciousness and integration are examined, and restated in a way that differentiates between several types of integration (i.e., spatiotemporal, multisensory, semantic integration, and integration of novel information). Review of existing empirical data (especially in the visual domain, because most studies focus on visual awareness[*]) suggests that there is no absolute dependency of integration on consciousness. Rather, the more complex or novel the stimuli, the more likely consciousness will be needed for integration to occur.

What precisely is meant by integration?

A phenomenological definition of integration is the combining of different features (e.g., parts of an object that are detected independently of each other [4]) into a unified percept (the binding problem [5]): for example, having a single experience of a black line rather than having two experiences, one of the color black and the other of a line. A cognitive definition of integration is the generation of a nonperceptual, abstract representation by associating distinct signals into a new one (e.g., when comparing the semantic congruency of two items and determining that '2' and '4' are both even numbers, or when constructing a new meaning by integrating two words such as 'honey' and 'moon' into a new word, 'honeymoon'). A formal, mathematical definition of integrated information is information that a system has as a whole, above and beyond the information possessed by the union of its parts [6,7].

Given the massively recurrent architecture of the brain, all neural processes are likely to involve some level of integration. Here, we specifically address integrative processes in which two or more distinct stimuli, or stimuli

Glossary

Unconscious processing: encoding of stimuli that remain below the threshold of awareness due to experimental or clinical conditions. That is, the stimulus is not consciously seen or heard or otherwise experienced. In this review, we focus on unconscious rather than implicit integration, in which the stimuli are perceived consciously but integrated without awareness of doing so. An example of such implicit integration is implicit sequence learning [93], where subjects implicitly integrate sequences of supraliminal stimuli, without explicitly declaring noticing such sequences.

Integrated information theory (IIT): identifies consciousness with information integration, so that the level of consciousness of a system is equivalent to its ability to integrate information over and above the information that is integrated by the union of its parts [94,95]. Importantly, however, in its current form, IIT does not include behavioral predictions about conscious versus unconscious processing [14].

Global neural workspace (GNW) theory: argues [12,25] that consciousness occurs when top-down attentional amplification mobilizes frontoparietal networks broadcasting neural signals throughout the brain. This makes those neural signals available to a variety of processes, including perceptual categorization, long-term memorization, linguistic processing evaluation, and intentional action. The theory draws from the Global Access Hypothesis in cognitive science [9,21], yet goes further in suggesting specific neural mechanisms that subserve global access.

Integration windows: the process of forming a unified representation from two or more features that are separated in space, in time, semantically, or in two different sensory modalities. The maximal distance between the integrated features defines the size of the integration window: for spatial integration windows (SIW), this distance refers to the actual distance in space between the integrated features. For temporal integration windows (TIW), it refers to the duration of the interval between the integrated events. For multisensory integration windows (MIW), it refers to the number of the integrated modalities, and for spatial processing integration windows (SPIW), it refers to the depth or level of complexity of semantic integration (see Box 1 for examples).

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[*]In this paper, we use the terms 'awareness' and 'consciousness' interchangeably.

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Table 1. Consciousness and integration in selected influential publications

Paper	Quote
Descartes, 1660 and 1664, respectively [1]	''[. . .] since our soul is not double, but one and indivisible, [. . .] the part of the body to which it is most immediately joined should also be single and not divided into a pair of similar parts''; AT III:124, CSMK 149, and ''it is only the latter figures which should be taken to be the forms or images which the rational soul united to this machine will consider directly when it imagines some object or perceives it by the senses''; AT XI:176, CSM I:106
Kant, 1781 [2]	''[. . .] the unity that the object makes necessary for us can be nothing other than the formal unity of consciousness in the synthesis of the manifold presentations. When we have brought about the synthetic unity in the manifold of intuition–this is when we say we cognise the object''; A105
James, 1890 [3]	''our mental states are composite in structure, made up of smaller states conjoined'', and ''We cannot even [. . .] have two feelings in mind at once'', p. 145 and p. 157, respectively.
Marcel, 1983 [17]	''Conscious perception requires a constructive act whereby perceptual hypotheses are matched against information recovered from records, and serves to structure and synthesize that information recovered from different domains. These processes are related to three aspects of phenomenal experience: awareness, unity of percepts, and selectivity'', Abstract.
Crick and Koch, 1990 [89]	''Our experience of perceptual unity suggests that the brain in some way binds together, in a mutually coherent way, all those neurons actively responding to different aspects of a perceived object [...] [neurons in different areas] are 'bound' together to carry a common label identifying them as neurons that jointly generate the perception of that specific face'', p. 269.
Singer, 1998 [91]	''In humans, only signals selected by attentional mechanisms reach the level of phenomenal awareness and only these selected signals can be integrated in episodic memories'', p. 1830.
Tononi and Edelman, 1998 [92]	''Categorizations of causally unconnected parts of the world can be correlated and bound flexibly and dynamically together inside consciousness but not outside it'', p. 247.
Damasio, 1999 [10]	''[. . .] a theory of consciousness should not be just a theory of how the brain creates integrated and unified mental scenes, although the production of integrated and unified mental scenes is an important aspect of consciousness, especially at its highest levels. Those scenes do not exist in a vacuum. I believe they are integrated and unified because of the singularity of the organism and for the benefit of that single organism. The mechanisms that prompt the integration and unification of the scene require an explanation'', pp. 18–19.
Engel, Fries, König, Brecht, and Singer, 1999 [8]	''[...] awareness seems to presuppose the capacity for structured representation, that it, the ability to achieve coherence of the contents of mental states and to establish specific relationships between representational items''.
Edelman and Tononi, 2000 [13]	''When we become aware of something [. . .] it is as if, suddenly, many different parts of our brain were privy of information that was previously confined to some specialized subsystem [. . .] the wide distribution of information is guaranteed mechanistically by thalamocortical and corticortical reentry, which facilitates the interactions among distant regions of the brain'', p. 148-149.
Kanwisher, 2001 [15]	''[...] in order for a focal neural representation to reach awareness it may have to be accessible to other parts of the brain [...] a conscious percept is not simply a disorganized soup of activated visual attributes, but rather a spatiotemporally structured representation in which visual attributes are associated with particular objects and events. The construction of a fully conscious percept may involve interactions between domain-specific systems for representing the contents of awareness (primarily in the ventral visual pathway) and domain-general systems (primarily in the dorsal pathway) for organizing those contents into structured percepts'', p. 109.
Dehaene and Naccache, 2001 [12]	''[. . .] a distributed neural system or 'workspace' with long-distance connectivity that can potentially interconnect multiple specialized brain areas in a coordinated, though variable manner [. . .] The global interconnection of those five systems can explain the subjective unitary nature of consciousness and the feeling that conscious information can be manipulated mentally in a largely unconstrained fashion'', pp. 13–14.
Varela, Lachaux, Rodriguez, and Martinerie, 2001 [18]	''[. . .] the large-scale integration of brain activity can be considered as the basis for the unity of mind familiar to us in everyday experience'', p. 237.
Baars, 2002 [9]	''Unconscious input processing is limited to sensory regions [. . .]Consciousness is needed to integrate multiple sensory inputs, presumably by mobilizing specialized functions like syntax, semantics, high-level visual knowledge, problem solving and decision making'', pp. 47–48.
Treisman, 2003 [5]	''Conscious access reflects binding. Conscious access in perception is always to bond objects and events [...] It [consciousness] combines information from many brain areas, and it binds that information to form integrated objects and events [...] Within this framework, binding is central to conscious experience'', pp. 97–98.
Goodale, 2004 [90]	''The representations constructed by the ventral stream play an essential role in the identification of objects an enable us to classify objects and events, attach meaning and significance to them, and establish their causal relations'', p. 1161.
Fahrenfort and Lamme, 2012 [11]	''A real perfect experiment would provide the neural mechanisms that explain functional properties of consciousness. Such mechanisms should be able to integrate contextual information across the visual field, making inferences about its input while resolving perceptual ambiguity. They should be able to dynamically group image elements together, creating perceptual unity and perceptual organization'', p. 138.
Koch, 2012 [16]	''Conscious states [. . .] are highly integrated [. . .]Whatever information I am conscious of is wholly and completely present to my mind. Underlying this unity of consciousness is a multitude of casual interactions among the relevant parts of my brain. If areas of my brain become fragmented, disconnected, and balkanized, as occurs under anesthesia, consciousness fades'', p. 125.

features, are combined into a whole. This combination may give rise to a percept comprising multiple features, to an assessment of the relations between features (e.g., similarity judgments at perceptual or semantic levels), or to the activation of a new representation (e.g., when the representation of '5' is activated by the addition of '2' and '3'). In all these cases, mere processing of each individual stimulus (although typically involving some integrative processes) does not by itself give rise to the integration product: it is only the combination of the stimuli and the mutual effect that each has on the processing of the other that constitutes an integration.

Previous claims about the relations between consciousness and integration

Almost every possible type of relation has been postulated with regards to consciousness and integration: some consider integration to be a prerequisite for any conscious experience [5,8], others claim that consciousness has an integrative function [9–12,100], and still others hold that integrated information is identical with information that is consciously accessible [7,13,14] [Integrated Information Theory (IIT); see Glossary]. The latter implies a relation of both necessity and sufficiency (i.e., integration is needed for consciousness, and consciousness is needed for integration). Let us examine the latter two possibilities.

Integration is needed for consciousness

At one end of the spectrum is the claim that integration (especially the perceptual one) is necessary for consciousness [8,15–18]. That is, there cannot be a conscious percept that is experienced as separate units of qualia rather than as a unified whole. The main thrust for this argument comes from the intuitive conceptualization of conscious experience as being holistic, undivided, and combining multiple sources of information across space, time, and sensory modalities. Yet, the experience of 'elemental percepts' such as spatially homogeneous fields of color (Ganzfeld) or single points of light, suggests that conscious experiences could vary in their degree of integration, and sometimes seemingly require relatively little integration (from an extrinsic perspective).

At present, it is not apparent how this claim could be addressed empirically. In the future, one could directly test the causal role of integration in perceptual awareness by inactivating all lateral and feedback connections, both local and global, reducing the nervous system to a feedforward one, and measuring the effect on subjects' conscious experience. Until such an empirical testing becomes possible, this claim should be regarded as a reasonable assertion that needs further validation.

Consciousness is needed for integration

Different functional roles have been assigned to consciousness, such as planning [19] or enabling flexible behavior [20–22] in the face of novel situations and tasks [12]. Common to all proposals is the notion that consciousness is required for the integration of multiple types of information, probably via long-range feedback connections [23,24]. Unconscious processing, on the other hand, is held to be encapsulated, informationally speaking [Global Neural Workspace theory (GNW)] [25,26]. But is consciousness really needed for integration? In addition, does this pertain to all types of integration? Surely, simple types of integration can be unconsciously performed; the detection of the orientation of a line, for example, involves integrating information across several receptive fields [27]. If so, perhaps consciousness is needed when the integration exceeds a certain level of complexity? To examine this possibility, we separately inspect four variants of this general claim that consciousness

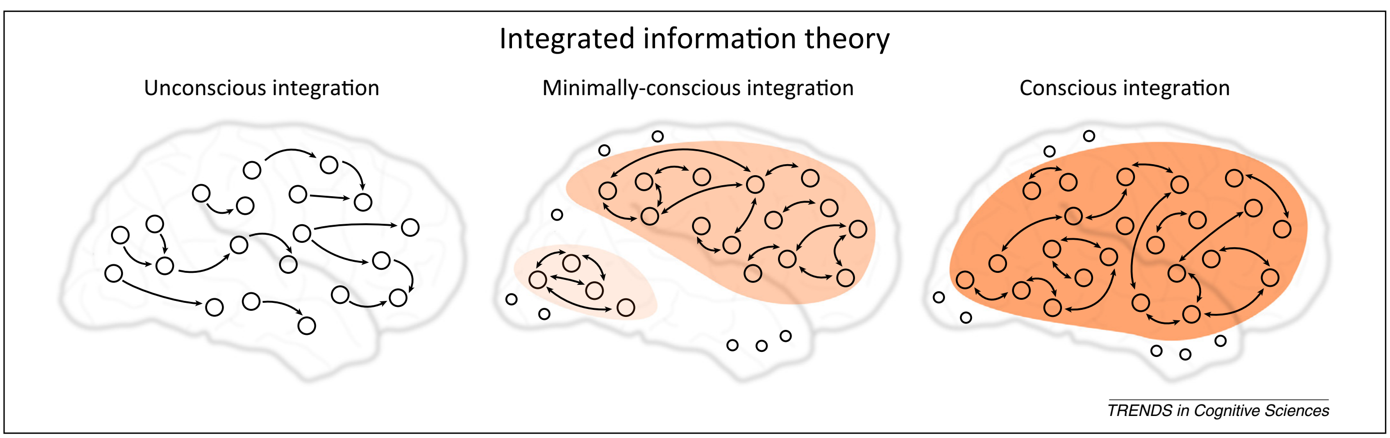

Figure 1. Possible neural basis of unconscious and conscious integration according to IIT: during conscious processing (right panel), the mechanisms (large circles) that integrate information above and beyond the union of their parts define a main complex (dark orange). This complex generates the subject's conscious experience, while receiving inputs and providing outputs to many smaller systems (small circles) that also receive inputs and provide outputs. By doing so, these systems can act as minor complexes; they also integrate information above and beyond the union of their parts, but to a lesser degree than the main complex. Thus, they do not causally participate in the conscious percept. Unconscious integration may be explained within the Integrated Information Theory (IIT) in two ways: first, it may be performed in a strictly feedforward manner (left panel), with no recurrent connections and accordingly with no conscious experience whatsoever. Such feedforward integration will rely on convergence mechanisms, in which, for example, the output of two neurons is projected to another neuron. This option seems unlikely, because such a feedforward architecture is highly inefficient and is not typical of neural organization. Second, what is commonly described as unconscious integration might be performed by some minor complex (depicted in light orange in the middle panel [103]), a subsystem that is integrating information alongside the main complex, yet to a much lesser extent (the main complex is depicted in darker orange in the middle panel; color intensity in this figure signifies the amount of integrated information, so that the main complex is darker than the minor one because it generates more integrated information). According to IIT, the main complex is the one that generates the greatest amount of integrated information (i.e., information that is over and above the information that is integrated by the subcomponents of that complex [14]). Accordingly, the major complex parallels the observer's conscious experience, whereas the minor complex is not consciously accessible to the observer (things may differ in a split-brain patient) but can influence his or her behavior (therefore, this should be regarded as minimally conscious integration rather than unconscious integration [14,103]).

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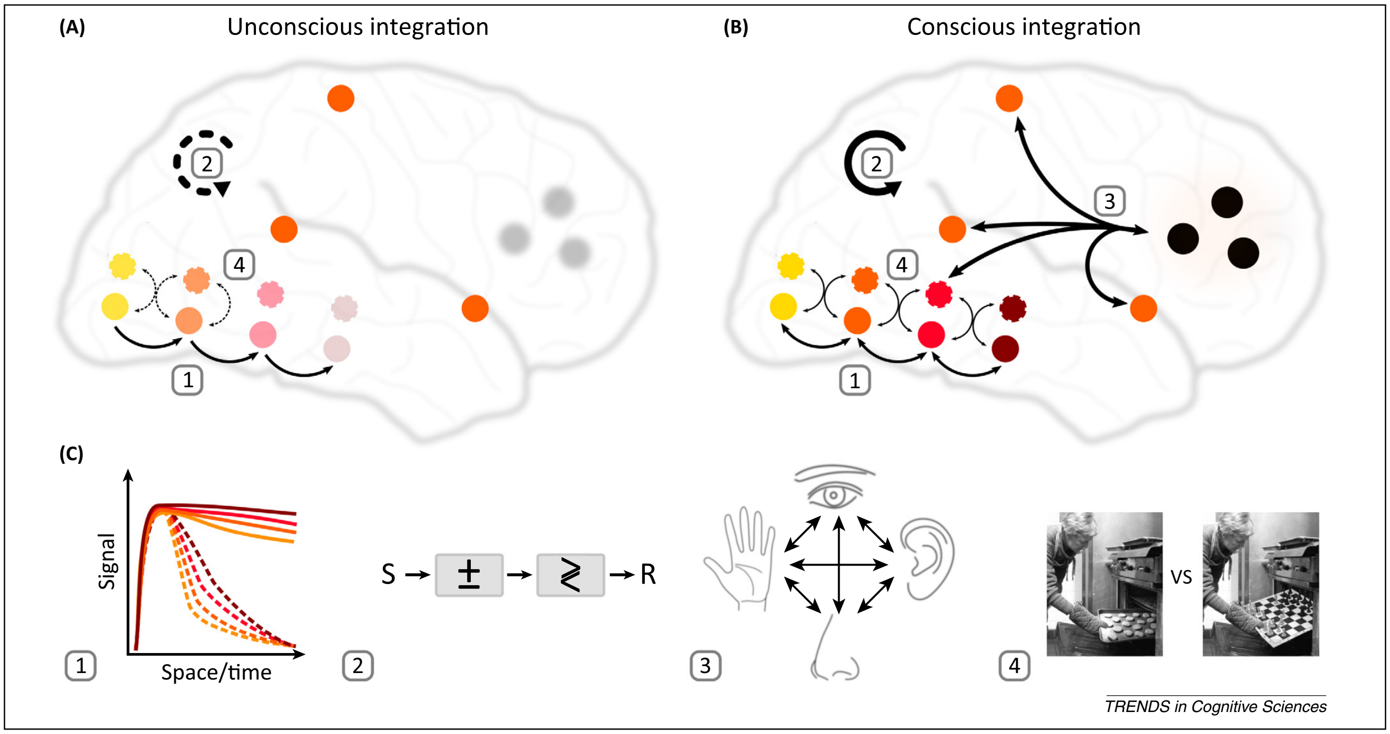

Figure 2. Possible neural basis of unconscious **(A)** and conscious **(B)** integration according to global neural workspace (GNW) theory. Lower row (**C**) depicts the different types of integration: 1. Spatiotemporal integration: in (**A**,**B**), spatial integration windows (SIWs) and temporal integration windows (TIWs) increase along the visual hierarchy (depicted as circles with a color gradient from yellow to brown), and shrink without awareness [depicted as a transparency gradient in (**A**)]. In C1, unbroken lines depict the neural signal at different hierarchical levels during conscious perception; this signal is maintained over space and/or time via feedback connections [double arrows in (**B**)], both locally and coming from parietal [101] or frontoparietal networks [25]. Broken lines in C1 represent the neural signal during unconscious perception that decreases with space and/or time. This decrease is faster at higher hierarchical levels. It occurs along the feedforward sweep [23,24] [simple arrows in (**A**)] and leads to the shrinkage of unconscious SIWs and TIWs). 2. Serial integration: in C2, two sequential operations (e.g., addition and comparison) are applied to the same stimulus (S) to produce a response (R). According to GNW, this requires information maintenance over time, for which consciousness is needed [looping arrow, solid line in (**B**)]. Empirical evidence for unconscious serial processing is still inconclusive [looping arrow, broken lines in (**A**)]. 3. Multisensory integration: in C3, signals from different sensory modalities converge into one integrated representation, supposedly via reciprocal connections between underlying sensory networks, or through feedback connections with a global workspace network [double arrows, unbroken lines in (**B**)], in which case it would be associated with consciousness ([9], but see [72]). 4. Semantic integration: during unconscious processing, horizontal projections within sensory areas may allow for the semantic integration of simple and closely related concepts [small semantic processing integration windows (SPIWs), represented by double arrows in posterior regions of the temporal cortex, broken lines in (**A**)], whereas feedback and stronger local connections during conscious processing are needed for integrating more complex and distant ones, like in C4, depicting visual scenes of different semantic contents [large SPIWs; double arrows in more anterior regions of the temporal cortex, unbroken lines in (**B**)]. In novel integration, unconscious integrative processes rely on preexisting networks formed during previous conscious experiences [double arrows, unbroken lines in (**A**)].

is needed for integration (for suggestions of the possible neural underpinnings of each of these variants according to IIT and GNW, see Figures 1 and 2, respectively).

Claim 1: consciousness is necessary for long-range but not short-range spatiotemporal integration

One of the most robust results in the field of unconscious perception is that subliminal stimuli defined across space and time can trigger specific neural and behavioral responses [28,29]. These responses are usually inferred from indirect measures of adaptation evoked by invisible stimuli (reviewed in [30,31]). In the spatial domain, evidence for unconscious processing has been found for not only single features (discrete components that can be detected independently of each other, such as color [32] or angular orientation [33], but also combinations of multiple features [34], such as superimposed orientations defining symbols [35], numbers [36], words [37], facial identities [38], facial expressions [39], natural scenes ([40,41], but see [42]), and even ensembles of objects or words (see Claim 2 below). All these processes involve integration, because the response induced by a combination of features is different from the summed responses evoked by each of these features separately.

The integrative processes described in the paragraph above are listed on an increasing scale in terms of the number and complexity of the integrated features, and also of the size of the spatial integration window (SIW): that is, the maximal distance in space between two features allowing their integration into a unified object or representation. Possibly then, the maximal SIW size may differ between conscious versus unconscious processing (see Box 1 for a suggested experiment that tests this hypothesis).

Such difference in integration size has been found in the temporal domain. At the perceptual level, temporal integration was demonstrated for continuous and apparent motion [43,44] as well as dynamic facial expressions [45]. At the cognitive level (i.e., not necessarily resulting in a phenomenal experience; see above), previous studies showed that perceptually invisible arithmetic instruction (e.g., add) can be applied to a set of two masked numbers with an ISI of 180 ms [46], that sequences of up to three crowded symbols can be unconsciously learned, with a temporal integration window (TIW) [47,48] of approximately 500 ms [49], and, most surprisingly, that words can be unconsciously associated even during much longer TIWs of 6–78 s [50]. By contrast, one study reported that subjects cannot unconsciously chain an operation with a subsequent one (i.e., add two numbers and then compare to 5) [51].

A direct comparison of TIW during conscious and unconscious processing was obtained by parametrically manipulating the temporal structure of motion of different complexities (i.e., apparent and biological motion) together with stimulus visibility [52]: this showed a decrease in TIW size during unconscious processing of both apparent and biological motion, perhaps reflecting the weak and transient amplitude of the underlying neural signals. Conversely, the stronger and more sustained signals associated with conscious perception, most likely achieved via recurrent activity [12,19,53], result in longer TIWs. Interestingly, TIW size also varied with stimulus complexity, such that it was larger for biological motion than for apparent dot motion. This implies that TIW size is dependent on both stimulus complexity and awareness, which might also happen in the spatial dimension.

Claim 2: consciousness is necessary for high-level but not low-level semantic integration

Although high- and low-level processing are often contrasted in psychology, no clear line delineates the two. Here, we define semantic processing as involving associative and/or past knowledge about the meaning of stimuli, or applying logical syntactic rules (i.e., judging for similarity, applying mathematic operators, etc.). Such processes are held to be unique to conscious processing (e.g., through parietal [101] or parietofrontal networks; see [12]).

Subjects can integrate subliminal stimuli and apply syntactic rules to them, either by judging their similarity (e.g., aa versus aA, or aD versus aA, see [54,55], and also [56]), by following a negation operator [57] or by applying arithmetic operations, including addition ([46,58], but see [59]), multiplication [60], subtraction of three numbers [59], and computing the average of three to five numbers [58]. High-level unconscious integration is also reflected in congruency effects, where invisible incongruent stimuli (e.g., a scene including an incongruent object [41] or an incongruent sentence such as 'I ironed coffee' [59]) either emerge faster into awareness [40,59] or impede subjects' performance on a subsequent stimulus [41].

Although these findings suggest that some forms of high-level semantic integration can be unconsciously performed, it remains hard to draw general conclusions about the scope of such integration; first, the variety of high-level processes being probed makes it harder to generalize across functions and mechanisms. Second, because many of these processes rest on more intuitive definitions of high-level functions (i.e., 'following rules' or 'semantic integration'), their operationalizations often vary profoundly between studies and rarely allow for direct manipulation of integration complexity. This emphasizes

Box 1. How to systematically study the relations between consciousness and integration.

Following our suggestion to conduct a systematic empirical investigation of the involvement of consciousness in different types of integration, we outline three relevant experiments.

Spatial integration

We propose to use ensemble coding [96,97] to test our hypothesis that the size of SIW increases with awareness and stimulus complexity. Ensemble coding is based on findings that subjects can extract summary statistics, such as the mean, from arrays of simultaneously presented objects (Figure IA, next page). Subjects are able to do so despite inattention [98] or visual masking [58,99]. These statistics can produce aftereffects [100] that serve as indirect measures of unconscious processing. The change in SIW size can be inferred by manipulating both the complexity and the visibility of ensembles of stimuli (Figure IA), and measuring aftereffects created by the summary statistics performed on these stimuli. If SIW indeed shrinks without awareness, integration outcomes should differ between the conscious and unconscious conditions. We expect that, for invisible stimuli, SIW will be small, allowing for ensemble coding of the angular orientation of the two central tilted bars only (in this case, leading to an average of 0°, because these bars have opposite tilts). By contrast, when visible, all four bars will fall within the larger SIW, leading to an average of 22.5° $[(45^\circ + 45^\circ + 45^\circ - 45^\circ)/4]$. Therefore, ensemble coding of visible and invisible tilted bars should elicit different aftereffects. Similarly, during unconscious processing, two shapes with a size of 2° and 4° (visual angle) would lead to an average of 3°, whereas during conscious processing, all four shapes would be averaged to a mean of 2.5°. Finally, with higher-level stimuli, unconscious processing that accesses the identity of all three symbols (12, 14, and the ambiguous stimulus 'I3') would create a representation of the number 13. By contrast, conscious processing would again enable larger SIW and, therefore, the summary representation based on all five symbols (12, 14, A, C, and I3), making the ambiguous stimulus 'I3' appear more as the letter B.

Multisensory integration

As opposed to previous studies that examined the integration of a supraliminal stimulus with a subliminal one [62–66,69–71], we propose here to suppress both stimuli from awareness and use priming to assess their integration (Figure IB). For example, one can present a subliminal prime that is a combination of a visual and an auditory digit, which could either be the same or different from each other. These two stimuli would be followed by a supraliminal target that is again a combination of two stimuli, this time a written and a spoken letter that can again be identical or different from each other. If unconscious multisensory integration occurs, subjects' performance for identical and/or different targets should be facilitated when preceded by identical and/or different primes, respectively. Crucially, in such a design, target performance can only be influenced by the combination of both stimuli, rather than their individual contents, as long as the target and prime do not share perceptual features.

Semantic integration

Here, we suggest manipulating the complexity of semantic relations between two stimuli (Figure IC), hypothesizing that lower-level relations would be unconsciously integrated, whereas higher-level ones will only be consciously integrated. To that end, we operationalize high-level relations as involving conceptual and associative knowledge, as opposed to low-level ones that rest on categorical knowledge. Accordingly, a pair of objects would be presented as prime, either consciously or unconsciously (using masking), followed by a visible pair that could either be the same or different from the prime. The objects within each pair could express low-level associative relations (e.g., two street signs), high-level associative relations (e.g., a street sign indicating multiple directions and a perplexed facial expression, suggesting that the person is at crossroads regarding some decision), or lack of associative relations (e.g., a street sign and a nest). If we are correct, there should be conscious facilitation of both high-level and low-level relations targets preceded by the same relations-type primes as compared with different ones. By contrast, during unconscious processing, only low-level relations (and not high-level ones) primes would facilitate the processing of similar targets.

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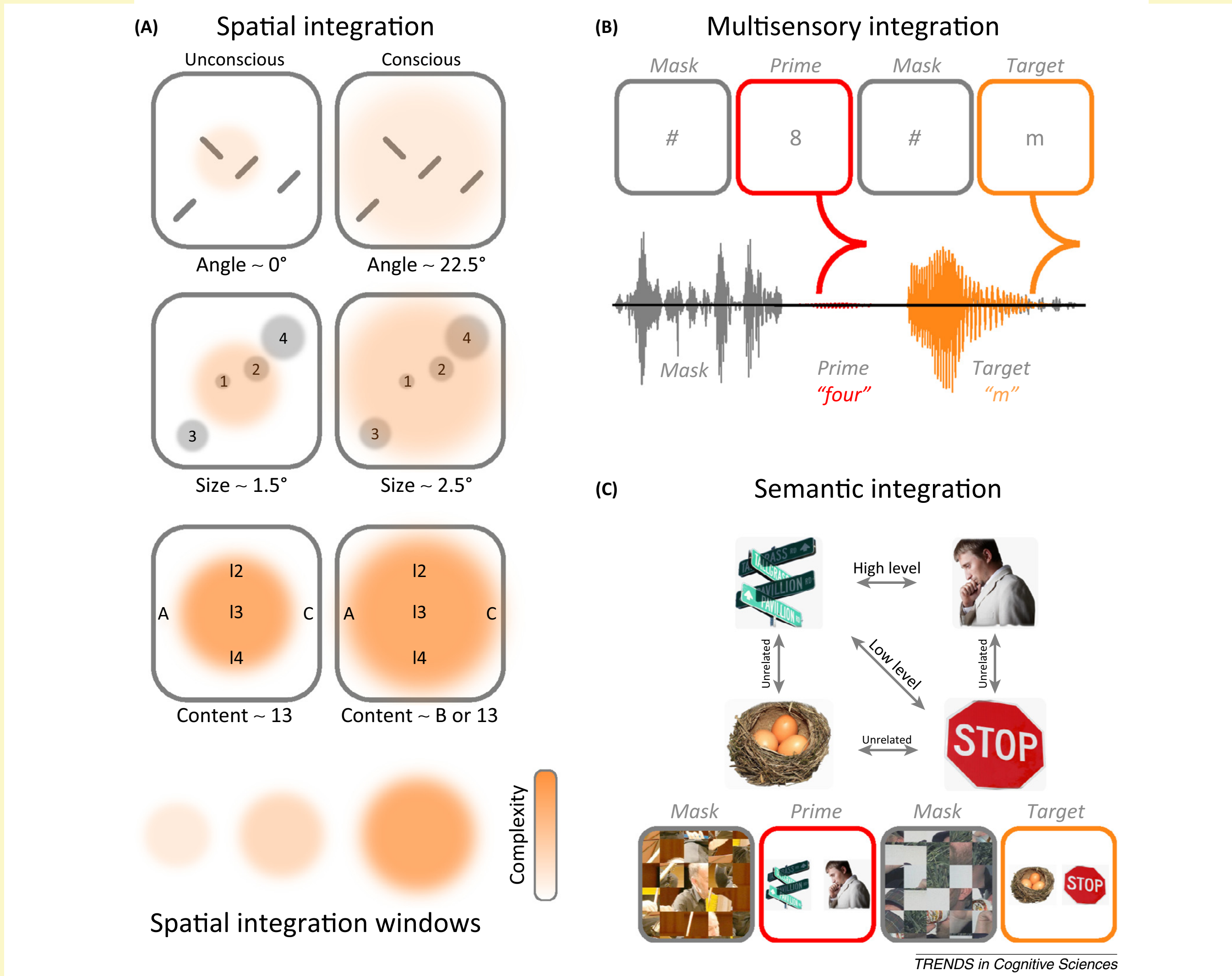

Figure I. Hypothetical experiments for quantifying the differences between conscious and unconscious integration. **(A)** Spatial integration windows (SIW) as a function of awareness and complexity: based on ensemble coding, sets of orientations, sizes, or symbols prime different values depending on the size of the SIW in which they are processed. We propose that the size of such windows increases both with stimulus complexity and visibility. **(B)** Multisensory integration windows (MIW) as a function of awareness: congruency judgments between an audio and a visual stimulus imply their integration into a single representation. Here, a congruent target (the written and pronounced letter 'm') is primed by an incongruent combination of a visual (the digit '8') and audio stimuli (the speech sound 'four'), both rendered subliminal using masking. If the two prime stimuli were integrated so that their incongruency was detected, performance for the congruent target should be slower. **(C)** Semantic processing integration windows (SPIW) as a function of awareness and complexity: semantic integration for low-level relations (e.g., two street signs), or high-level and/or metaphorical relations (e.g., a street sign indicating multiple direction and a perplex facial expression) is measured through priming during conscious and unconscious processing (here, using masking: related and/or unrelated primes should facilitate the processing of related and/or unrelated targets, respectively). We predict that such effects will only be found for low-level relations in the absence of awareness, as opposed to conscious processing that allows for the detection of high-level associations as well as low-level ones.

again the need for a quantitative approach where the depth of unconscious semantic processing integration windows (SPIW) is systematically manipulated, akin to the SIW–TIW approach above (for suggestions, see Box 1).

Claim 3: consciousness is necessary for multisensory integration

It has been proposed that multisensory integration requires consciousness [9]. Although TIW, SIW, and even SPIW (in some cases) may depend on horizontal connections within a sensory cortical area, multisensory integration windows (MIW) are likely to rely on long-range connections between different sensory cortices, in addition to potential multisensory convergence zones, such as the superior temporal sulcus or the posterior parietal cortex [61]. Thus far, it has only been shown that the processing of an invisible stimulus is affected by the processing of congruent and incongruent consciously perceived stimuli in the auditory [62–68], tactile [69], proprioceptive [70], or olfactory [71] modalities (for review, see [102]). This, by itself, can be accommodated within the global access hypothesis [9]: information about the supraliminal stimulus spreads to all modules, including the unconsciously activated visual one, enabling its comparison with the invisible stimulus. Thus, only an experiment where both stimuli are unconsciously presented can truly probe unconscious MIW. Such unconscious integration of tones and odors was reported during sleep [72], when unconscious association of these stimuli produced behavioral conditioning. However, no study to date has manipulated awareness of multimodal stimuli in awake subjects, where stringent measures of awareness can be obtained (Box 1).

Most multisensory studies above relied on congruency effects, akin to the semantic integration ones described in the previous section: when a subliminal stimulus was incongruent with a concurrent supraliminal stimulus, the former was either less readily detected (e.g., [65,68,70,73]), or it slowed down subjects' subsequent responses [64]. Yet interestingly, the very same stimuli that showed such congruency effects were found not to be integrated into a new perceptual experience: during conscious processing, incongruent sound and visual lip movement typically produce the McGurk effect [74], an auditory illusion in which subjects report hearing a new sound (e.g., when the sound 'ba' is played together with the lip movement 'ma', subjects report hearing 'na'). When the visual lip movement was rendered invisible using continuous flash suppression, it slowed subjects' responses to a subsequent target, but did not evoke the McGurk effect; subjects reported hearing the sound that was actually played [64]. In the next section, we explain this dissociation by examining the claim that consciousness is needed to integrate new information.

Claim 4: consciousness is necessary for novel but not for previously learned integration

The abovementioned congruency effects (i.e., a drop in performance following an incongruent combination of stimuli) may actually reflect the role of consciousness in integrating new, as opposed to familiar, associations. Arguably, integration of subliminal stimuli might fail when these defy previous expectations [40], or do not belong to associations that were already consciously formed by means of synaptic potentiation, for example [12]. According to this suggestion, when subjects are confronted by elements that are commonly integrated (e.g., congruent scenes and sentences, congruent speech sounds and lip movements), these can be unconsciously processed by relying on associations acquired and strengthened through multiple previous exposures. By contrast, during unconscious processing of incongruent stimuli, no such mechanism is available, because it was not formed during previous conscious processing. For scene–object relations, for example, object-level sensory information that does not match associative knowledge triggered by the gist of the scene (e.g., a scene of basketball players playing with a watermelon rather than a basketball; see [75]), may render object identification [76], and possibly also object–scene integration, harder [77]. The difficulty of identifying the object or integrating it with the scene then affects subjects' performance: it raises the attentional saliency of the scene [78,79], causing it to emerge into awareness sooner [40,59], or to hinder the processing of a subsequent stimulus [64,80]. Importantly, these effects on performance, usually taken as evidence for unconscious integration, may only reflect the difficulty to processes the incongruent stimulus, rather than its integration with the scene. In other words, for such effects to be found, subjects do not necessarily need to integrate unconsciously the basketball players with the watermelon and process their incongruency. Rather, it may be that during unconscious processing, the mismatch between the gist of the basketball game and the green color of the watermelon makes it impossible for subjects to even identify that this is a watermelon. Accordingly, the scene is not unconsciously integrated into a unified, coherent percept or representation, but is rather not unconsciously comprehensible for the subject, probably leading to it requiring further conscious inspection. This hypothesis predicts that the incongruent associations are not integrated into unified percepts in the absence of awareness, in line with the lack of unconscious McGurk effect [64].

This claim naturally begs a direct empirical investigation. A demonstration of the role of previous conscious exposure in unconscious integration comes from a study that probed subjects' ability to integrate unconsciously chess configurations and determine whether they entail a direct threat to the king (e.g., in a 3×3 chess board where the king is displayed in the upper left corner, a rook in the upper right corner leads to a check-mate, whereas a knight displayed in the upper right corner does not). Masked configurations induced subliminal priming, but only for expert chess players, and not novice chess players [81] (note, however, that both experts and novice players failed to show priming when asked to detect whether a knight or a rook were displayed on a white or black field). Furthermore, closer inspection of some of the studies above that reported unconscious semantic integration similarly reveals that they also included conscious trials, where subjects were consciously exposed to the task and the stimuli either before being unconsciously presented with them, or during the same session (e.g., [56,57,59]). Thus far, only a few studies imply that new associations can be formed, and only between a subliminal stimulus and a supraliminal reward/punishment [82–85]. Here again, integration might rely on the conscious processing of the reward or the punishment, and on preexisting conditioning mechanisms. In addition, the stimuli sets in these experiments are relatively small and are extensively repeated, making them less and less novel as the experiment progresses. A few studies do imply that new associations can be unconsciously formed between word pairs [50,86], sequence of symbols [49], and tones and odors during sleep [72], but none parametrically manipulated novelty during conscious and unconscious processing.

Concluding remarks: what can be said about the relations between consciousness and integration?

Although the experiments reviewed here suggest that consciousness is not necessary for some types of integration, it nevertheless has an important role in integrative processes, in accordance with prominent theories in the field (IIT [7,14] and GNW [12,25]): consciousness enables information integration over extended distances (SIW) and durations (TIW), and facilitates integration over higher semantic levels (SPIW), multiple modalities (MIW), and the formation of novel associations. We suggest that, for the latter, consciousness has an enabling role, by establishing integration mechanisms that do not require stimulus consciousness on later trials. The data indicate that the scope of unconscious integrative processes is more limited, and effect sizes are smaller in comparison to conscious ones (akin to lower-level forms of visual adaptation, where tilt and motion aftereffects decrease in amplitude during unconscious processing [87]). Notably, however, this interpretation of effect size decrease is mitigated by the fact that most experimental manipulations of consciousness involve some decrease of stimulus strength (see [88] for potential solutions).

Taken together, the demonstrations of unconscious integration are not sufficient to support the claim that consciousness has no functional role in integration (this basically amounts to claiming that the function of legs has nothing to do with movement, because legless organisms can still move [88]). Rather, they imply that some integrative process can take place without awareness, whereas others cannot. We propose a few experiments that can directly test these limitations, including the size of TIW, the multimodal span of MIW, and the extent of SPIW (Box 1). These could serve as the next steps towards a more detailed account of the relations between consciousness and integration.

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References
1 Adam, C. and Tannery, P., eds (1964–1974) *Oeuvres de Descartes*, Paris
2 Kant, I. (1998) *Critique of Pure Reason*, Cambridge University Press
3 James, W. (1890) *The Principles of Psychology*, Macmillan
4 Suchow, J.W. and Pelli, D.G. (2013) Learning to detect and combine the features of an object. *Proc. Natl. Acad. Sci. U.S.A.* 110, 785–790
5 Treisman, A.M. (2003) Consciousness and perceptual binding. In *The Unity of Consciousness: Binding, Integration, and Dissociation* (Cleeremans, A., ed.), pp. 95–113, Oxford University Press
6 Griffith, V. and Koch, C. (2012) Quantifying synergistic mutual information. *arXiv* 1205.4265
7 Balduzzi, D. and Tononi, G. (2008) Integrated information in discrete dynamical systems: motivation and theoretical framework. *PLoS Comput. Biol.* 4, e1000091
8 Engel, A.K. *et al.* (1999) Temporal binding, binocular rivalry, and consciousness. *Conscious. Cogn.* 8, 128–151
9 Baars, B.J. (2002) The conscious access hypothesis: origins and recent evidence. *Trends Cogn. Sci.* 6, 47–52
10 Damasio, A.R. (1999) *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*, Harvest Books
11 Fahrenfort, J.J. and Lamme, V.A.F. (2012) A true science of consciousness explains phenomenology: comment on Cohen and Dennett. *Trends Cogn. Sci.* 16, 138
12 Dehaene, S. and Naccache, L. (2001) Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79, 1–37
13 Edelman, G.M. and Tononi, G. (2000) *A Universe of Consciousness: How Matter Becomes Imagination*, Basic Books
14 Tononi, G. (2013) Integrated information theory of consciousness: an updated account. *Arch. Ital. Biol.* 150, 290–326
15 Kanwisher, N. (2001) Neural events and perceptual awareness. *Cognition* 79, 89–113
16 Koch, C. (2012) *Consciousness – Confessions of a Romantic Reductionist*, MIT press
17 Marcel, A.J. (1983) Conscious and unconscious perception: an approach to the relations between phenomenal experience and perceptual processes. *Cogn. Psychol.* 15, 238–300
18 Varela, F. *et al.* (2001) The brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2, 229–239
19 Crick, F. and Koch, C. (2003) A framework for consciousness. *Nat. Neurosci.* 6, 119–126
20 Cheesman, J. and Merikle, P. (1984) Priming with and without awareness. *Percept. Psychophys.* 36, 387–395
21 Baars, B.J. *et al.* (2013) Global workspace dynamics: cortical 'binding and propagation' enables conscious contents. *Front. Psychol.* 4, 200
22 Searle, J.R. (1992) *The Rediscovery of Mind*, MIT Press
23 Lamme, V.A.F. (2006) Towards a true neural stance on consciousness. *Trends Cogn. Sci.* 10, 494–501
24 Lamme, V.A.F. and Roelfsema, P.R. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579
25 Dehaene, S. and Changeux, J.P. (2011) Experimental and theoretical approaches to conscious processing. *Neuron* 70, 200–227
26 Dehaene, S. *et al.* (2014) Toward a computational theory of conscious processing. *Curr. Opin. Neurobiol.* 25, 76–84
27 Hubel, D.H. and Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160, 106
28 Kouider, S. and Dehaene, S. (2007) Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 362, 857–875
29 Lin, Z.C. and He, S. (2009) Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211
30 Kim, C.Y. and Blake, R. (2005) Psychophysical magic: rendering the visible 'invisible'. *Trends Cogn. Sci.* 9, 381–388
31 Tsuchiya, N. and Koch, C. (2005) Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101
32 Schmidt, T. (2000) Visual perception without awareness: priming responses by color. In *Neural Correlates of Consciousness: Empirical and Conceptual Questions* (Metzinger, T., ed.), pp. 157–179, The MIT Press
33 Blake, R. and Fox, R. (1974) Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249, 488–490
34 Treisman, A.M. and Gelade, G. (1980) A feature-integration theory of attention. *Cogn. Psychol.* 12, 97–136
35 Vorberg, D. *et al.* (2003) Different time courses for visual perception and action priming. *Proc. Natl. Acad. Sci. U.S.A.* 100, 6275–6280
36 Dehaene, S. *et al.* (1998) Imaging unconscious semantic priming. *Nature* 395, 597–600
37 Dehaene, S. *et al.* (2001) Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4, 752–758
38 Kouider, S. *et al.* (2009) Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cereb. Cortex* 19, 13–23
39 Whalen, P.J. *et al.* (2004) Human amygdala responsivity to masked fearful eye whites. *Science* 306, 2061
40 Mudrik, L. *et al.* (2011) Integration without awareness: expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770
41 Mudrik, L. and Koch, C. (2013) Differential processing of invisible congruent and incongruent scenes: a case for unconscious integration. *J. Vis.* 13, 24
42 Faivre, N. and Koch, C. (2014) Inferring the direction of implied motion depends on visual awareness. *J. Vis.* 14, 4
43 Rajimehr, R. *et al.* (2004) Adaptation to apparent motion in crowding condition. *Vision Res.* 44, 925–931
44 Kaunitz, L. *et al.* (2011) Unseen complex motion is modulated by attention and generates a visible aftereffect. *J. Vis.* 11, 10 11–19
45 Faivre, N. *et al.* (2012) Nonconscious emotional processing involve distinct neural pathways for pictures and videos. *Neuropsychologia* 50, 3736–3744
46 Ric, F. and Muller, D. (2012) Unconscious addition: when we unconsciously initiate and follow arithmetic rules. *J. Exp. Psychol. Gen.* 141, 222–226
47 VanRullen, R. and Koch, C. (2003) Is perception discrete or continuous? *Trends Cogn. Sci.* 7, 207–213
48 Blake, R. and Lee, S.H. (2005) The role of temporal structure in human vision. *Behav. Cogn. Neurosci. Rev.* 4, 21–42
49 Atas, A. *et al.* (2013) Nonconscious instrumental learning from crowded sequences. *Psychol. Sci.* http://dx.doi.org/10.1177/0956797613499591
50 Reber, T.P. and Henke, K. (2012) Integrating unseen events over time. *Conscious. Cogn.* 21, 953–960

51 Sackur, J. and Dehaene, S. (2009) The cognitive architecture for chaining of two mental operations. *Cognition* 111, 187–211
52 Faivre, N. and Koch, C. (2014) Temporal structure coding with and without awareness. *Cognition* 131, 404–414
53 Fisch, L. *et al.* (2009) Neural 'ignition': enhanced activation linked to perceptual awareness in human ventral stream visual cortex. *Neuron* 64, 562–574
54 Van Opstal, F. *et al.* (2011) Setting the stage subliminally: unconscious context effects. *Conscious. Cogn.* 20, 1860–1864
55 Van Opstal, F. *et al.* (2010) Unconscious task application. *Conscious. Cogn.* 19, 999–1006
56 Lin, Z. and Murray, S.O. (2014) Unconscious processing of an abstract concept. *Psychol. Sci.* 25, 296–298
57 Armstrong, A.M. and Dienes, Z. (2013) Subliminal understanding of negation: unconscious control by subliminal processing of word pairs. *Conscious. Cogn.* 22, 1022–1040
58 Van Opstal, F. *et al.* (2011) Rapid parallel semantic processing of numbers without awareness. *Cognition* 120, 136–147
59 Sklar, A.Y. *et al.* (2012) Reading and doing arithmetic nonconsciously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619
60 García-Orza, J. *et al.* (2009) '2 x 3' primes naming '6': evidence from masked priming. *Atten. Percept. Psychophys.* 71, 471–480
61 Driver, J. and Noesselt, T. (2008) Multisensory interplay reveals crossmodal influences on 'sensory-specific'brain regions, neural responses, and judgments. *Neuron* 57, 11–23
62 Chen, Y.C. and Spence, C. (2010) When hearing the bark helps to identify the dog: semantically-congruent sounds modulate the identification of masked pictures. *Cognition* 114, 389–404
63 Chen, Y.C. *et al.* (2011) Crossmodal constraints on human perceptual awareness: auditory semantic modulation of binocular rivalry. *Front. Psychol.* 2, 212
64 Palmer, T.D. and Ramsey, A.K. (2012) The function of consciousness in multisensory integration. *Cognition* 125, 353–364
65 Alsius, A. and Munhall, K.G. (2013) Detection of audiovisual speech correspondences without visual awareness. *Psychol. Sci.* 24, 423–431
66 Ngo, M.K. and Spence, C. (2010) Crossmodal facilitation of masked visual target identification. *Atten. Percept. Psychophys.* 72, 1938–1947
67 Doi, H. and Shinohara, K. (2013) Unconscious presentation of fearful face modulates electrophysiological responses to emotional prosody. *Cereb. Cortex* http://dx.doi.org/10.1093/cercor/bht282
68 Lupyan, G. and Ward, E.J. (2013) Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 110, 14196–14201
69 Lunghi, C. *et al.* (2010) Touch disambiguates rivalrous perception at early stages of visual analysis. *Curr. Biol.* 20, R143–R144
70 Salomon, R. *et al.* (2013) Posing for awareness: proprioception modulates access to visual consciousness in a continuous flash suppression task. *J. Vis.* 13, 1–8
71 Zhou, W. *et al.* (2010) Olfaction modulates visual perception in binocular rivalry. *Curr. Biol.* 20, 1356–1358
72 Arzi, A. *et al.* (2012) Humans can learn new information during sleep. *Nat. Neurosci.* 15, 1460–1465
73 Chen, Y.C. and Spence, C. (2011) The crossmodal facilitation of visual object representations by sound: evidence from the backward masking paradigm. *J. Exp. Psychol. Hum. Percept. Perform.* 37, 1784–1802
74 McGurk, H. and MacDonald, J. (1976) Hearing lips and seeing voices. *Nature* 264, 746–748
75 Mudrik, L. *et al.* (2010) ERP evidence for context congruity effects during simultaneous object-scene processing. *Neuropsychologia* 48, 507–517
76 Biederman, I. *et al.* (1982) Scene perception: detecting and judging objects undergoing relational violations. *Cogn. Psychol.* 14, 143–177
77 Bar, M. (2004) Visual objects in context. *Nat. Rev. Neurosci.* 5, 617–629
78 Mudrik, L. *et al.* (2011) Scene congruency biases binocular rivalry. *Conscious. Cogn.* 20, 756–767
79 Underwood, G. *et al.* (2008) Is attention necessary for object identification? Evidence from eye movements during the inspection of real-world scenes. *Conscious. Cogn.* 17, 159–170
80 Kiesel, A. *et al.* (2009) Playing chess unconsciously. *J. Exp. Psychol. Learn. Mem. Cogn.* 35, 292–298
81 Pessiglione, M. *et al.* (2008) Subliminal instrumental conditioning demonstrated in the human brain. *Neuron* 59, 561
82 Raio, C.M. *et al.* (2012) Nonconscious fear is quickly acquired but swiftly forgotten. *Curr. Biol.* 22, R477–R479
83 Seitz, A.R. *et al.* (2009) Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron* 61, 700–707
84 Knight, D.C. *et al.* (2003) Expression of conditional fear with and without awareness. *Proc. Natl. Acad. Sci. U.S.A.* 100, 15280–15283
85 Reber, T.P. *et al.* (2012) Unconscious relational inference recruits the hippocampus. *J. Neurosci.* 32, 6138–6148
86 Blake, R. *et al.* (2006) Strength of early visual adaptation depends on visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4783–4788
87 Lau, H. (2009) Volition and the functions of consciousness. In *Cognitive Neurosciences* (5th edn) (Gazzaniga, M.S., ed.), pp. 1191–1200, MIT Press
88 Crick, F. and Koch, C. (1990) Towards a neurobiological theory of consciousness. *Semin. Neurosci.* 2, 273–304
89 Goodale, M.A. (2004) Perceiving the world and grasping it: dissociations between conscious and unconscious visual processing. In *The Cognitive Neurosciences III* (3 edn) (Gazzaniga, M.S., ed.), pp. 1159–1172, MIT Press
90 Singer, W. (1998) Consciousness and the structure of neuronal representations. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 353, 1829–1840
91 Tononi, G. and Edelman, G.M. (1998) Consciousness and the integration of information in the brain. In *Consciousness: At the Frontiers of Neuroscience, Advances in Neurology* (Jasper, H.H. *et al.*, eds), pp. 245–279, Lippincott-Raven
92 Nissen, M.J. and Bullemer, P. (1987) Attentional requirements of learning: evidence from performance measures. *Cogn. Psychol.* 19, 1–32
93 Tononi, G. (2008) Consciousness as integrated information: a provisional manifesto. *Biol. Bull.* 215, 216–242
94 Tononi, G. (2010) Information integration: its relevance to brain function and consciousness. *Arch. Ital. Biol.* 148, 299–322
95 Ariely, D. (2001) Seeing sets: representation by statistical properties. *Psychol. Sci.* 12, 157–162
96 Alvarez, G.A. (2011) Representing multiple objects as an ensemble enhances visual cognition. *Trends Cogn. Sci.* 15, 122–131
97 Oriet, C. and Brand, J. (2012) Size averaging of irrelevant stimuli cannot be prevented. *Vision Res.* 79, 8–16
98 Choo, H. and Franconeri, S. (2010) Objects with reduced visibility still contribute to size averaging. *Atten. Percept. Psychophys.* 72, 86–99
99 Corbett, J.E. *et al.* (2012) An aftereffect of adaptation to mean size. *Vis. Cogn.* 20, 211–231
100 Dehaene, S. *et al.* (2014) Toward a computational theory of conscious processing. *Current Opinion in Neurobiology* 25, 76–84
101 Frässle, S. *et al.* (2014) Binocular Rivalry: Frontal Activity Relates to Introspection and Action But Not to Perception. *The Journal of Neuroscience* 34, 1738–1747
102 Deroy, O. *et al.* (2014) Multisensory constraints on awareness. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369, 20130207
103 Oizumi, M. *et al.* (2014) From the phenomenology to the mechanisms of consciousness: integrated information theory 3.0. *PLoS Comput. Biol.* 10, e1003588