

pulvinar, Plm, that is interconnected with MT is likely unique to primates.

Thus, area MT and Plm may have evolved in concert. Possibly the caudomedial portion of the inferior pulvinar was dominated throughout by superior colliculus inputs in the ancestors of primates, and the Plm territory was first isolated from the rest of PI by an expanded input from the retina, replacing, in part, the role of the superior colliculus in activating a part of temporal visual cortex, the antecedent of MT. As a later step in this proposed evolution, V1 projections to MT emerged slightly later in development, reducing or eliminating the role of the retinal inputs to Plm in vision, with Plm eventually becoming a satellite nucleus of MT, receiving its major input from MT while projecting back to MT. Thus, the results of Warner *et al.* [9] provide insights into the ways in which area MT and surrounding cortex might have evolved in the immediate ancestors of primates.

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## Cognitive Neuroscience: Integration of Sight and Sound outside of Awareness?

A recent study found that auditory and visual information can be integrated even when you are completely unaware of hearing or seeing the paired stimuli — but only if you have received prior, conscious exposure to the paired stimuli.

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Many of the objects and events we encounter during our everyday lives are made up of distinct blends of auditory and visual information: dogs barking, motors whining, people talking. Even though the physical signals conveying those qualities are fundamentally different — for example, photic energy versus acoustic energy — our brain seamlessly integrates, or ‘binds’, this

information into a coherent perceptual Gestalt. The unitary nature of these multisensory perceptual experiences raises an important question in the context of prevailing theories of consciousness [1]: specifically, can such binding take place prior to the emergence of consciousness, or is it an emergent property of consciousness? Earlier work has indicated that audible sounds can impact invisible pictures suppressed from awareness during binocular rivalry [2], but can auditory

and visual signals interact when both are presented outside of awareness? A recent study by Faivre *et al.* [3] provides an answer to this question by unequivocally demonstrating the interaction of subthreshold auditory and visual cues. Left unanswered, however, is whether this interaction represents genuine multisensory integration or, instead, arises from interactions at amodal, semantic levels of analysis (Figure 1).

In the new study [3], participants were briefly presented a priming stimulus made up of a pair of digits — one presented as a visual stimulus and the other as an auditory stimulus — that were sometimes identical (for example, a spoken ‘2’ and a printed ‘2’) and other times were not (for example, a spoken ‘8’ and a printed ‘2’). This prime was then followed by an audio-visual pair of target letters that were either identical or not. Participants had to judge whether this

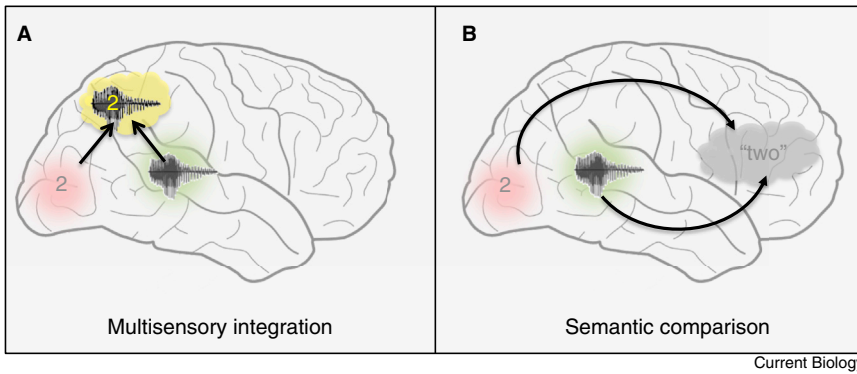


Figure 1. Schematic representations of alternative ways in which auditory and visual information may interact in the priming design of Faivre *et al.* [3].

(A) Multisensory integration involves combination of sensory signals from visual cortex (denoted by red) and auditory cortex (denoted by green), resulting in an integrated representation in regions of multisensory cortex (for example, superior temporal and/or parietal regions, denoted by yellow). (B) With semantic comparison, two independent sensory representations, one auditory (green) and the other visual (red), signify the same object and, thus, activate a common semantic concept (the abstract concept of the number, represented by 'two', in this case) within higher level, cognitive areas.

second pair was the same (for example, a spoken and printed 'b') or different (for example, a spoken 'm' and a printed 'b'). Crucially, the first audio-visual digit pair — the priming pair — was presented at subthreshold intensities and durations. This clever design meant that the pair of primes and the pair of targets could either be congruent (both pairs the 'same' or both pairs 'different') or incongruent (one pair the 'same' and the other pair 'different'). With this design, by contrasting reaction times to target-relationship identification as a function of whether or not that pair was congruent with the prime-relationship, the authors were able to determine whether the subthreshold primes were integrated (as evidenced by reduced reaction times). Indeed, a congruency effect would be dependent on the successful determination of the semantic relationship between the subliminal auditory and visual digits. The authors also assessed priming under conditions where the auditory and visual digits were suprathreshold.

Remarkably, following repeated exposures to primes presented at suprathreshold levels, subliminal pairs were able to impact reaction times for judging the auditory-visual target relationship, an outcome implying that these subliminal auditory and visual signals were integrated outside of awareness. But what is being integrated in such a situation? Is it the low-level visual and acoustic features of the priming stimuli (thus arguing for

true multisensory integration)? Or is it the higher-order semantic features of the stimuli, thus arguing for a process based on comparison of congruence of semantic information arising from two sources, rather than on genuine integration?

The results from the Faivre *et al.* [3] study do not allow us unequivocally to answer this question. They do, however, provide important clues suggesting that the process may be taking place at the semantic level. These clues are founded in one of the hallmark features of multisensory integration — the concept of inverse effectiveness — whereby the multisensory gain is most pronounced when the paired unisensory signals are weak [4,5]. If the priming signals were being integrated in a multisensory manner, one would expect that the weaker the primes, the greater the gain when they were integrated, and thus, the larger the effects sizes. Conversely, if the results were entirely driven by sensory-independent semantic congruency priming, we would expect that the stronger the priming signal, the bigger the effect size.

Although inverse effectiveness was not directly tested, there are several informative aspects of the experimental results that bear on the interpretation. The first emerges from a comparison of the results of experiments 1 and 2 with those of experiment 3. In the first two experiments the auditory (experiment 1) and visual (experiment 2) primes

were presented at levels sufficiently strong to render them unequivocally suprathreshold, while in experiment 3 they were both presented subliminally. Despite these differences in stimulus effectiveness, the priming effects were comparable in magnitude for each of these three experiments. The second clue emerges from the first three experiments, where participants were exposed to suprathreshold primes before subliminal testing, to the results from experiment 4, where subliminal testing was *not* preceded by exposure to suprathreshold prime pairs. Subliminal priming worked in experiments 1–3 but did not work in experiment 4. Framed in the context of inverse effectiveness, it is not at all obvious why prior exposure would be necessary before weak stimuli could be integrated in order to facilitate performance. Thus, this pattern of results also seems incompatible with the concept of inverse effectiveness, but compatible with semantic priming.

We believe that, in addition to effectiveness manipulations, another key set of principles governing multisensory integration may be used in future work to further differentiate between unconscious multisensory integration and unconscious semantic comparison. It is well established that the spatial and temporal structure of paired sensory cues — here, the spoken and written digits — are a major determinant of the probability that these cues will be integrated. Stimuli in close spatial and temporal correspondence have a high likelihood of being integrated [6]. In contrast, semantic priming should be independent of the spatial location at which stimuli are delivered, as well as more dependent upon the relative timing between primes and targets (rather than on the timing between the primes themselves) [7].

In our opinion, the jury is still out on the question of the nature of the information being combined when a subliminal auditory digit is presented together with a subliminal visual digit within a priming paradigm. We believe that this question can be resolved by exploiting several of the classic features of multisensory integration. Regardless of the resolution of that question, however, the study by Faivre *et al.* [3] stands as a provocative contribution to the question of binding and consciousness by definitively

showing that the property of congruence between auditory and visual information can be established outside of awareness.

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## Sensorimotor Control: Retuning the Body–World Interface

A new study reveals the action of a rapid process by which our perceptual systems adapt to improve the localization of touches when our limbs are in novel postures.

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As we move through and explore our worlds, our bodies and limbs come into momentary contact with a complex and ever-changing array of objects and surfaces. Somehow the brain has to assemble these, often fleeting, tactile sensations into representations of the world and the bodily self [1,2]. Perhaps one of the greatest challenges to this achievement is movement: every time our limbs change posture, the relation between tactile coordinates on the skin surface and locations in the external environment changes. To take a relatively straightforward example, if you cross your arms a tactile stimulus on your left hand will, rather than occurring as usual on the left side of your body, now occur on the right (Figure 1). In maintaining a coherent representation of the world and the body, how does the brain respond to the numerous transient postures of the body and limbs which occur from moment to moment across our daily routines?

A number of studies in recent years have shown that when locating a touch we rapidly take the current position of the limbs into account to remap it to its location in the external world (for example, [3–5]). This process is not perfect, however: we tend to make more mistakes locating touches when our arms are

in unusual postures [6–9]. Similarly, we tried typing this dispatch with crossed hands, but quickly gave up. There is a reason why we don't usually do things with crossed hands: our sensorimotor systems are set up in some way to expect our bodies to have a canonical alignment (Figure 1) [10]. In a new study reported in this issue of *Current Biology*, Azañón *et al.* [11] show that the brain takes this problem seriously. They find that when a new atypical limb posture is adopted — in this case, the crossed-hands posture — tactile localisation improves rapidly, so that reliable performance benefits are seen even across sequential trials.

#### Ways of Adapting to New Limb Postures in Adults and Across Development

We certainly need adaptive processes like that demonstrated by Azañón *et al.* [11]. Given the variety of postures through which our bodies and limbs move from moment to moment, our ability to make sense of the tactile stream of information presented to the nervous system seems almost miraculous. But spare a thought also for the poor developing infant and child: not only do infants have to cope with the wide range of postures which their bodies can adopt (and which increase dramatically in early life), but the

canonical layout of their limbs is also changing — infants can gain as much as 2.5 cm in height within just two days [12].

But what precisely is it that our brains do to improve our performance in new or atypical body layouts? One possibility is that we rapidly change assumptions about where our limbs usually rest in space — that is, that we update our representations of canonical body layout. Another is that we hone our representations of where exactly our hands are right now. Whilst one might want to question whether there is any reason to posit separate contributions of current and prior information to hand representation, research from our lab [13–15] with human infants suggests that there might be justification for such a distinction.

Six-month-old infants find it more difficult to locate touch stimuli when their hands are crossed [13], a finding which points to the influence of a representation of canonical body posture even at this tender age. But when investigating how the six-month-old brain processes tactile stimuli, we could find no evidence that this age group integrated into somatosensory processing the current posture of the limbs, as do adults and ten-month-old infants [4,5,14]. Thus, in six-month-olds, the canonical layout of the body influences responses to tactile stimuli without any evident ability to remap tactile location according to the current position of the arms [15].

Studies which have examined the role of experience on tactile localisation in unfamiliar postures, prior to Azañón *et al.* [11], have demonstrated relatively slow