

Touch disambiguates rivalrous perception at early stages of visual analysis

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Binocular rivalry is a powerful tool to study human consciousness [1]: two equally salient stimuli are imaged on the retinae, but at any given instant only one is consciously perceived, the other suppressed. The suppression takes place early, probably in V1 [2]. However, a trace of the suppressed signal has been detected along the dorsal visual pathway (BOLD responses [3]) and demonstrated with psychophysical experiments. The suppressed image of a rotating sphere during rivalry is restored to consciousness when the observer actively controls the rotation [4] and a similar effect on the suppressed signal has been shown for motion perception [5] and reflexive eye movements (see Supplemental References). Here, we asked whether cross-modal sensory signals could selectively interact with rivalrous visual signals that are analyzed at a very early stage, probably V1. An auditory stimulus, when attended, can influence binocular rivalry, extending dominance times for a congruent visual stimulus [6]. Tactile information can also disambiguate unstable visual motion [7] and can fuse with vision to improve discrimination (e.g. slant) [8]. Our results indicate that a haptic oriented stimulus can disambiguate visual perception during binocular rivalry of gratings of orthogonal orientation, not only by prolonging dominance but also by curtailing suppression of the visual stimulus of matched orientation. The effect is selective for the spatial frequency of the stimuli, suggesting that haptic signals interact with early visual representations to enhance access to conscious perception.

We tested whether touch could interfere with the dynamics of binocular rivalry by having subjects explore haptically a grooved stimulus

of the same orientation as one of the two rival visual stimuli. Visual stimuli were orthogonal Gabor Patches (oriented vertically or horizontally), displayed alternatively to the two eyes; the haptic stimulus was a sinusoidal grooved Plexiglas, matched in spatial frequency with the visual gratings; subjects could see neither their hand nor the stimulus they touched (for more details see Supplemental Methods). While reporting the perceived orientation of the visual stimulus, participants were required at random intervals to touch (with circular movements of the right thumb) the haptic stimulus and to release it after a brief period of ~3 sec (short enough to avoid deployment of attention [6] and adaptation to the haptic stimulus, but long enough to allow tracing its effect on the slow dynamic of binocular rivalry; see also Supplemental Data). For each touch period, visual and haptic stimuli were unpredictably parallel to each other or orthogonal (Figure 1A).

The probability of maintaining or switching perception was influenced by touch (see Supplementary Methods). Haptic stimulation

disambiguated visual perception both by promoting dominance of the visual stimulus with the same orientation and by reducing suppression. When the orientations of the haptic and visual stimuli were orthogonal, the conditional probability of switching perception (green bar in Figure 1C), re-establishing congruency of visual and haptic stimuli orientation, increased by 35% compared to parallel stimulation (orange bar in Figure 1C) and by 20% compared to no touch periods (white bar in Figure 1C). This suggests that the haptic signal boosted the suppressed stimulus signal provoking a perceptual switch, leading the parallel stimulus to revert to perceptual dominance. Conversely, when haptic and visual stimuli were parallel, the conditional probability of maintaining dominance of the visual stimulus increased by 34% compared to the orthogonal visuo-haptic stimulation and by 20% compared to no touch periods (Figure 1B). Hence the duration of dominance as well as of the suppression of a rival visual stimulus can be substantially affected by

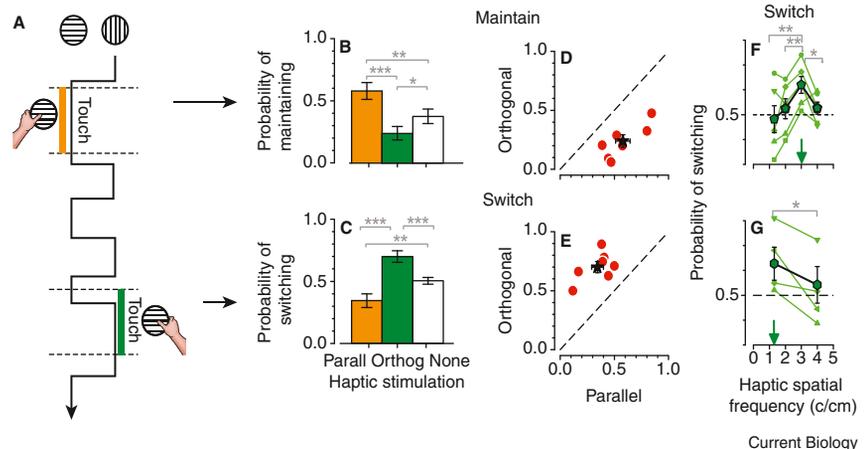


Figure 1. Experimental procedure and results.

(A) The perception of an example subject, alternating between vertical and horizontal phases. Exploring a parallel haptic stimulus (orange line) extended the phase, but exploring an orthogonal stimulus shortened it (green line). (B,C) Conditional probability of maintaining (B) or switching (C) perception given parallel (parall, orange), orthogonal (Orthog, green) or no haptic stimulation (None, white). (D,E) Conditional probability of maintaining (D) or switching (E) perception for orthogonal versus parallel visuo-haptic orientation of the individual subjects. Parallel stimulation increased the probability of maintaining dominance, while orthogonal visuo-haptic stimulation increased the probability of switching. (F,G) Haptic spatial frequency selectivity of the switch probability for the orthogonal visuo-haptic stimulation. The visual spatial frequency was 3 c/cm (1.6 cpd) for (F) and 1.3 c/cm (0.7 cpd) for (G). Green lines show the individual subjects and the black line the average; dotted lines indicate the switching rate during the no-touch periods. For both visual frequencies, the switch probability peaks when visual and haptic spatial frequencies are matched (green arrow). * refers to $p < 0.05$, ** refers to $p < 0.01$, *** refers to $p < 0.001$.

the presentation of a congruent haptic stimulus (see also Figure S2). The individual data reported in Figures 1D and E show that the effect is consistently observed in all tested subjects. By repeating the experiment using visual and haptic stimuli of different spatial frequencies we found that the effect of touch on the suppressed visual stimulus was selective for matched visuo-haptic spatial frequencies. Figures 1F and G show the average modulation of the probability of switching perception for the orthogonal visuo-haptic stimulation as a function of the haptic spatial frequency, together with the individual subjects' results. The probability peaks when the visual and the haptic stimuli have the same spatial frequency (equal to 3 c/cm in F and to 1.3 c/cm in G), demonstrating that the tuning is not a mere consequence of the haptic spatial frequency selectivity.

Our results demonstrate that a visual stimulus, rendered invisible by binocular rivalry suppression, can nonetheless revert to consciousness when boosted by a concomitant haptic signal of congruent orientation and spatial frequency. When there is a conflict between the orientation of the visual and the haptic stimuli, vision switches to the congruent orientation, indicating that the system uses the haptic signal to resolve binocular rivalry. Touch and visual signals are optimally fused in many tasks [8] (see also Supplemental References), but the fusion is not mandatory, consistent with the prevailing view that it is mediated by high-level associative multisensory cortex. Also during binocular rivalry, fusion is usually not mandatory, given that other sensory modalities interact specifically with the dominant stimulus. For example, an attended looming auditory stimulus can prolong the dominance of a congruently moving visual stimulus [6], but not rescue it from suppression. In the case of bistable perception of an ambiguously rotating sphere, a haptic signal (rotating globe) can prolong the dominance of the congruent direction but not shorten its suppression [7]. The present results are the first to show that touch can make visible an otherwise unseen stimulus, suggesting

mandatory fusion. In principle, the effect could be mediated by attention or imagination. However, the spatial frequency selectivity of the observed effect (with the peak effect changing with the spatial frequency of the visual stimulus) is inconsistent with attentive or other non-specific effects, and points strongly to early interactions between haptic and visual signals. V1 neurons have the narrowest spatial frequency tuning of visual neurons and could mediate the effect reported here, which requires a bandwidth of less than 1 octave.

Suppression during binocular rivalry is very strong in primary visual cortex, but a trace of the suppressed stimulus can be detected along the dorsal pathway [3]. This residual trace can interact with the dominant rival stimulus, changing its appearance [5], but not restore the suppressed stimulus to perception. The only reported case of restoring the suppressed stimulus involves voluntary manipulation [4]. However, it is known that attention is allocated to the target of a successful motor act, and this could affect the strength of the suppression. In fact, attention is one of the two factors that consistently influences the strength of binocular rivalry suppression, the other being contrast [9]. Interestingly, both the contrast of the stimulus and attention are known to modulate primary visual cortex activity. In order to boost a suppressed visual signal, therefore, it is very likely that the haptic signal must reach early visual cortex, in line with previous evidence from blind patients, in which V1 is recruited for tactile processing [10]. It has recently been proposed that reorganization of the visual cortex in the blind reinforces pre-existing connections between somatosensory and visual cortex, the tactile input to visual cortex being normally masked by the robust visual input. In the absence of visual inputs (for example, during prolonged blindfolding [10]), these connections become more effective. We propose that the same happens during binocular rivalry suppression, revealing the non-visual roles of the occipital cortex by unmasking tactile inputs. Our findings strongly suggest that not only can haptic signals modulate activity at the earliest stages of

visual processing (consistent with recent neurophysiological evidence; see Supplemental References), but that these signals influence low level visual perception, opening the way to consciousness for an otherwise invisible stimulus.

Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)02134-4](http://www.cell.com/current-biology/supplemental/S0960-9822(09)02134-4)

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