

Early Interaction between Vision and Touch during Binocular Rivalry

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Abstract

Multisensory integration is known to occur at high neural levels, but there is also growing evidence that cross-modal signals can be integrated at the first stages of sensory processing. We investigated whether touch specifically affected vision during binocular rivalry, a particular type of visual bistability that engages neural competition in early visual cortices. We found that tactile signals interact with visual signals outside of awareness, when the visual stimulus congruent with the tactile one is perceptually suppressed during binocular rivalry and when the interaction is strictly tuned for matched visuo-tactile spatial frequencies. We also found that voluntary action does not play a leading role in mediating the effect, since the interaction was observed also when tactile stimulation was passively delivered to the finger. However, simultaneous presentation of visual and tactile stimuli is necessary to elicit the interaction, and an asynchronous priming touch stimulus is not affecting the onset of rivalry. These results point to a very early cross-modal interaction site, probably V1. By showing that spatial proximity between visual and tactile stimuli is a necessary condition for the interaction, we also suggest that the two sensory spatial maps are aligned according to retinotopic coordinates, corroborating the hypothesis of a very early interaction between visual and tactile signals during binocular rivalry.

Keywords

Binocular rivalry, multisensory integration, vision, touch, psychophysics

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1. Introduction

When two dissimilar images are presented simultaneously to the eyes they do not merge into a unique percept, but engage a competition for visual awareness so that only one image is perceived at a time; the other, although displayed on the retina, is perceptually suppressed. The competition generates continuous perceptual alternations despite the constant physical stimulation, termed binocular rivalry (see *On Binocular Rivalry*; Levelt, 1965). The fact that conscious perception can change with no accompanying changes to the physical stimulus makes binocular rivalry a fascinating tool to investigate the neural correlates of visual consciousness (Koch, 2007).

Although binocular rivalry is thought to result from neural activity at various stages of visual processing (Blake and Wilson, 2011), neural activity from the suppressed visual image is already attenuated at the earliest stages of visual analysis: LGN (Haynes *et al.*, 2005), monocular and binocular neurons in V1 (Keliris *et al.*, 2010; Tong and Engel, 2001). The suppression is thought to increase in depth at higher levels of visual processing (Nguyen *et al.*, 2003). No trace of the neural activity associated with the suppressed visual stimulus can be detected along the ventral pathway (Tong *et al.*, 1998), in agreement with the fact that face adaptation is disrupted when the adaptor is perceptually suppressed (Moradi *et al.*, 2005) (for a review on binocular rivalry suppression, see Lin and He, 2009). Only stimuli processed by the dorsal pathway or conveying an emotional content (Yang *et al.*, 2007) have been found to escape binocular rivalry suppression. Examples are given by BOLD activity associated with suppressed images of tools in parietal area (Fang and He, 2005); the influence on the dominant motion direction by the suppressed direction (Alais and Parker, 2006; Andrews and Blakemore, 1999) and the fact that voluntarily controlling the motion direction of a suppressed rotating sphere can restore it to consciousness (Maruya *et al.*, 2007).

In a previous study (Lunghi *et al.*, 2010) we used binocular rivalry to investigate cross-modal interactions between haptic and visual signals. We showed that a haptic signal can rescue the visual stimulus congruent in orientation from binocular rivalry suppression, and that the interaction between visual and tactile signals during binocular rivalry is strictly tuned for matched visuo-haptic spatial frequencies. From both these sets of evidence, we inferred that the haptic signal boosts the suppressed visual signal at the very early stages of visual processing, probably V1 or V2. This hypothesis is consistent with the existence of projections from the polysensory areas of the temporal lobe to V1 in monkeys (Falchier *et al.*, 2002), with the evidence that the primary visual cortex of rats responds to tactile discrimination of novel objects, and its activity correlates with tactile discrimination performance in an aperture discrimination task (Vasconcelos *et al.*, 2011). Consistently, in normal sighted

humans, BOLD studies show that primary visual cortex is activated during exploration of tactile dots (Merabet *et al.*, 2007). V1 is recruited for tactile processing in blind patients (Sadato *et al.*, 1996) and in normal sighted humans after prolonged blindfolding (Merabet *et al.*, 2008). We therefore suggested that visual instability during binocular rivalry can reveal the somatosensory connections to primary visual cortex that are normally masked by the strong visual input.

The present study shows that the interaction between visual and tactile signals during binocular rivalry requires spatial overlap between visual and tactile stimuli, suggesting that already at the level of V1 — the putative site of the interaction — there must be a dynamic alignment between the two sensory spatial maps. In addition, we show that the effect does not require active exploratory action or an attentional allocation of the subject. However, the spatial frequency of the texture of the object must be closely matched.

2. Materials and Methods

2.1. Subjects

Ten subjects (three males, average age 28 ± 3.9 years), including one of the authors, participated in the experiment (subject AS took part only in two conditions); all had normal or corrected-to-normal vision, normal stereo acuity (Frisby Stereotest (Sasieni, 1978)), with no strong eye dominance. Subjects gave informed consent. The experiments were carried out along the principles laid down in the declaration of Helsinki, and with approval of the relevant ethics committees.

2.2. Apparatus and Stimuli

The experiment took place in a dark and quiet room. Visual stimuli were created in MATLAB using PsychToolbox (Brainard, 1997), and displayed on a 24-inch monitor (Acer LCD GD245HQ), hung 37 cm over an opaque mirror. Observers viewed the reflection of the monitor at a distance of 20 cm from the mirror through anaglyph red-blue goggles (right lens blue, left lens red). Responses were recorded through the computer keyboard. Visual stimuli were two oblique orthogonal red and blue gratings (orientation: $\pm 45^\circ$, size: 3° , SF 2 cpd or 3.5 cpd, contrast 30%), surrounded by a white smoothed circle, presented on a black uniform background in central vision. Peak luminance of the red grating was matched with the physical peak luminance of the blue one (2.13 cd/m^2). The edges of the mirror were hidden by a black cloth, minimizing visual references. The tactile stimulus was a sinusoidal grating (size: 3 cm, SF: 2 c/cm) created with a 3D printer (Dimension Elite SST, Stratasys, Inc., Eden Prairie, MN). The stimulus was attached to a prop that could be moved 3 cm back and forth under computer control with a linear trajectory at constant

speed of 2.5 cm/s. The motor and the stimulus prop were positioned under the mirror, with the tactile stimulus being at the same distance of the monitor (37 cm from the mirror), so that the visual stimulus was projected exactly on the tactile one. The orientation of the tactile stimulus could be changed by lever. Figure 2F illustrates the set-up.

2.3. Task and Procedure

2.3.1. Binocular Rivalry

Each observer participated in five 180-s experimental sessions \times five experimental conditions for a total time of 75 min, over different days. The three main tactile conditions were *active exploration*, *passive touch*, *touch away*. Active exploration and passive touch were tested also with non-matched visuo-tactile spatial frequencies (Visual SF: 3.5 cpd, Tactile SF: 2 c/cm). The order of the different conditions was randomized for every observer.

After an acoustic signal (beep) the visual binocular rivalry stimuli appeared. Participants reported their visual perception by continuously pressing with the left hand one of two keys (up or down arrows) of the computer keyboard. They were instructed to track color alternation; at each experimental session the orientation of the rival stimuli was swapped between the eyes. As assessed in training binocular rivalry sessions and in debriefing sessions, mixed percepts occurred for very brief periods, only during perceptual transitions, and their frequency remained constant across conditions.

In the *active exploration* condition, during the observing period, at approximately regular intervals, observers were asked by the experimenter (verbal instruction) to explore the tactile stimulus with their right index finger performing a constant translational movement, until the experimenter gave a stop signal (average touch period: 2.5 ± 0.15 s). At each touch period the orientation of the tactile stimulus was manipulated by the experimenter alternating the clockwise and counterclockwise orientations following preset random generated sequences (the orientation of the stimulus was unpredictable at each touch period). Touch periods timing and stimulus orientation were recorded by the experimenter by holding the proper mouse button.

The *touch away* condition was identical to the *active exploration* except that the tactile stimulus was positioned 30 cm away (on the horizontal axis) from the location corresponding with the visual stimulus (center). At each touch period the observer accomplished a movement with the arm to reach the tactile stimulus (average touch period: 2.6 ± 0.14 s) and then went back to the resting position (centered on the visual stimulus).

During the *passive touch* condition, the tactile stimulus was drifted 3 cm back and forth at 0.83 Hz. Observers wore insulating headphones to attenuate the sound of the motor, and kept their right index finger stationary on a foam rubber guide. The dynamics of the experiment were the same, except

that touch periods were delivered by the experimenter using a lever that elevated the tactile stimulus to touch the finger pad of the participant (average touch period: 2.6 ± 0.15 s, 2.8 ± 0.14 s for the mismatched spatial frequency condition).

2.3.2. Tactile Priming

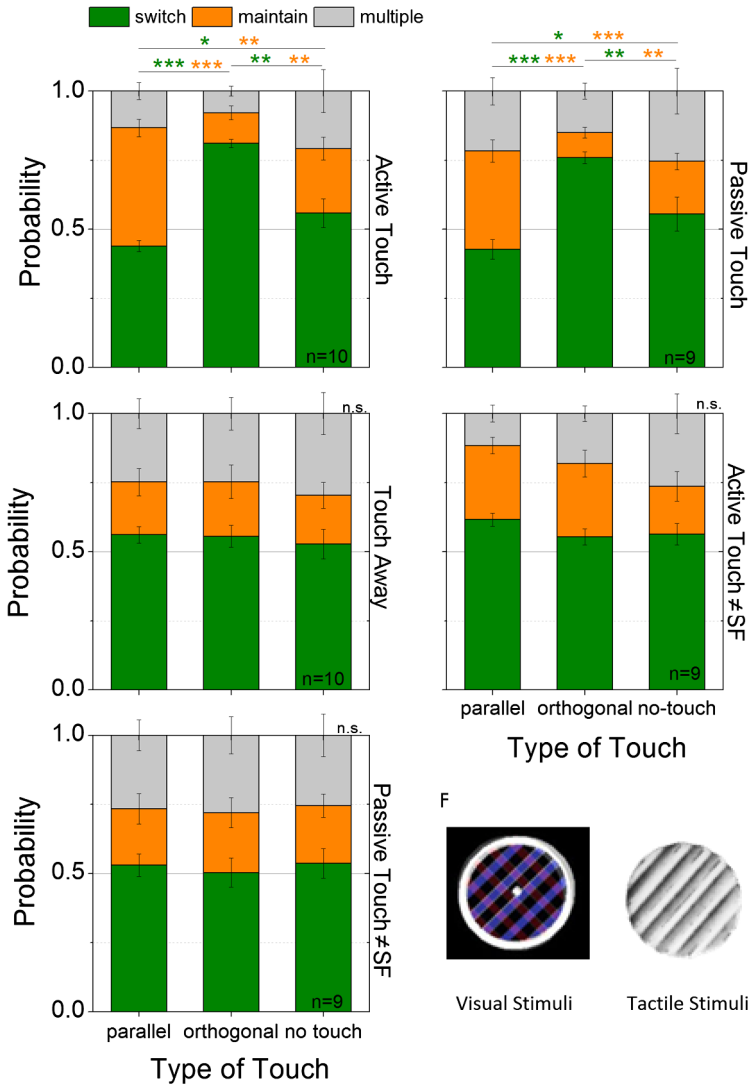
Two tactile priming durations (10 and 3 s) were tested in separate blocks comprising 30 consecutive trials. When cued by the acoustic signal (beep), together with the written instruction to 'touch', observers started to actively explore the tactile stimulus with the right index finger. After 10 or 3 s (depending on the condition), a second beep sounded and the observers raised their finger from the stimulus, and the visual stimuli were displayed (red-blue gratings) for 3 s. The temporal delay from the beep signaling the end of touch and the presentation of the visual stimuli was set to 500 ms, but the actual separation between the end of touch and the visual stimulus depended on the RT of the subjects. Using the computer keyboard, observers were asked to report their first percept (red or blue) by appropriate key pressing. A 2 s break was interleaved between trials, during which the experimenter changed the orientation of the tactile stimulus following preset random generated sequences. At each trial the orientation of the visual grating was swapped between the eyes.

3. Results

3.1. Interaction between Visual and Tactile Signals during Binocular Rivalry

We measured the effect of touch on binocular rivalry for active exploration and passive tactile stimulation conditions in separate blocks. In order to reduce the possibility of response bias, in all conditions observers were asked to track the color of the dominant stimulus (red or blue) and not the orientation (that was randomly associated with one of the two at every experimental block). In the conditions requiring active exploration of the tactile stimulus, observers were asked at random intervals to explore the tactile stimulus with a horizontal movement of the right index finger. In the passive touch conditions, the right index finger of the observer was stationary on a prop and tactile stimulation was passively delivered with the tactile patch moving at a constant velocity of 2.5 cm/s. The touch periods were brief (average 2.5 s) and interleaved with vision-only stimulation; at each touch period the visual and the tactile stimuli could randomly be parallel or orthogonal to each other.

We first computed the probability of switching, maintaining the same percept or switching more than once for the different conditions of visuo-tactile stimulation: parallel, orthogonal or, as a control condition, for period of visual only stimulation of comparable duration (Fig. 1A–E).



In the active-touch condition, when the visual and the tactile stimuli were parallel, the probability of maintaining the same percept for the whole touch period (Fig. 1A, orange bars) increased by 32% compared with orthogonal visuo-tactile stimulation and by 20% compared with no-touch periods. When the visual and the tactile stimuli were orthogonal, the probability of switching (Fig. 1A, green bars) increased by 37% compared with parallel visuo-tactile stimulation and by 25% compared with no-touch periods. Consistent with our previous report (Lunghi *et al.*, 2010), active tactile stimulation influenced the dynamics of binocular rivalry, both by prolonging dominance and by curtailing suppression of the visual percept parallel to the tactile stimulus. Interestingly, the same result held for the passive-touch condition (Fig. 1B): during parallel visuo-tactile stimulation the probability of maintaining the same percept for the whole touch period increased by 27% compared with orthogonal visuo-tactile stimulation and by 17% compared with no-touch periods; similarly during orthogonal visuo-tactile stimulation the probability of switching increased by 32% compared with parallel visuo-tactile stimulation and by 21% compared with no-touch periods. In the passive condition the tactile signal was purely sensory: voluntary attention to the finger and active action were not involved (the finger was stationary in a resting position with tactile stimulation passively delivered by the experimenter, his/her only task was to report visual perception).

Spatial proximity is known to be crucial for cross-sensory integration (Gepshtein *et al.*, 2005). To test if it is also crucial in modulating the visual rivalry, we repeated the experiment by placing the tactile stimulus 30 cm away

Figure 1. Average probabilities across touch conditions. The average probabilities of switching visual perception once (green bar), maintaining the same visual percept (orange bar) or switching more than once during a touch period (gray bar), depending on the type of visuo-tactile stimulation (parallel, orthogonal or no-touch periods of comparable duration), plotted for the different experimental conditions (the error bars represent s.m.e.). Tactile stimulation influenced the dynamics of binocular rivalry both during Active- and Passive-Touch conditions (Panel 1A–B): the probability of switching was significantly higher when the visual percept was orthogonal to the tactile stimulus, while the probability of maintaining the same visual percept for the whole touch period was significantly higher for parallel visuo-tactile stimulation (paired *t*-test, $n = 10$, two tailed, $\alpha = 0.025$, $* = p \leq 0.025$, $** = p \leq 0.01$, $*** = p \leq 0.001$). When the visual and the tactile stimuli were in different locations, tactile stimulation had no effect on binocular rivalry (Panel 1C): none of the probabilities differed across visuo-tactile conditions. Tactile stimulation was also ineffective when the visual and the tactile stimuli were mismatched in Spatial Frequency, both for Active (Panel 1D) and Passive (Panel 1E) touch. Panel 1F shows the visual and the tactile stimuli. The visual stimuli were orthogonal red and blue gratings oriented at $\pm 45^\circ$, presented separately to the eyes through anaglyph red and blue goggles; the tactile stimulus was an engraved sinusoidal grating matched in Spatial Frequency with the visual stimuli (2 c/cm).

from the visual stimulus apparent location; at each touch period observers were trained to reach the tactile stimulus, explore it with the right index finger and, after the stop signal, go back to the resting position aligned with the visual stimulus. We introduced the movement of the arm to re-set proprioception, that is known to drift in the dark (Desmurget *et al.*, 2000). When the visual and the tactile stimulus occupied different locations (touch away condition) tactile stimulation did not influence the dynamics of binocular rivalry: none of the probabilities differs across visuo-tactile conditions (Fig. 1C). Touch was ineffective also when the visual and the tactile stimulus were mismatched in spatial frequency at the same location (i.e. spatial frequency of the visual stimulus was 3.5 c/cm, while the tactile spatial frequency was 2 c/cm): maintaining, switching (once or more than once) are equally likely across visuo-tactile conditions both for active exploration of the tactile stimulus (Fig. 1D) and passive tactile stimulation (Fig. 1E).

A factorial 5×3 repeated measures ANOVA revealed a main effect of the type of tactile stimulation (parallel, orthogonal, or none) both for the probability of maintaining the same percept for the whole touch period ($F = 17.704$, $p \leq 0.001$) and for the probability of switching once ($F = 8.639$, $p \leq 0.01$), but not for the probability of switching more than once ($F = 0.955$, $p = 0.406$). A main effect of experimental condition was found only for the probability of performing one switch during the touch period ($F = 3.085$, $p \leq 0.05$). A significant interaction of the two factors (experimental condition \times type of touch) was found both for the probability of performing one switch during the touch period ($F = 23.458$, $p \leq 0.001$) and for the probability of maintaining the same percept during the whole touch period ($F = 6.806$, $p \leq 0.001$), but not for the probability of performing multiple switches ($F = 1.975$, $p = 0.065$). The probability of maintaining and performing one switch significantly differed for the different type of tactile stimulations only for the active and passive touch conditions, as revealed by a paired two tailed t -test (Fig. 1).

We further analyzed the time-course of the effect of touch on binocular rivalry by computing the instantaneous probability of seeing the visual stimulus parallel to the tactile stimulus as a function of time elapsed from the onset of touch (Fig. 2A–E). All touch periods (independently from the type of visuo-tactile stimulation) were aligned at time zero, so that the probability trace starts at chance level (with some random variability). In the active-touch condition (Fig. 2A), the average probability increased over time and reached statistical significance 0.7 s after the onset of touch, peaked at 1.7 s and then slowly decayed over time back to chance 1.5 s after the end of tactile stimulation. In the passive-touch condition, the probability trace reached statistical significance 1 s after the onset of touch, peaked at 2.3 s and reverted to chance 1 s after the end of tactile stimulation. The time-course of the effect was slower than that

for the active touch condition, while the decay of the effect was faster. Consistently with the average probabilities, when the visual and the tactile stimuli were in different locations (Fig. 2C) or were mismatched in spatial frequency (Fig. 2D–E), the average probability trace was nearly flat and never reached a statistically significant difference from chance level, indicating again that tactile stimulation did not interact with binocular rivalry under these conditions.

Taken together these results show that spatial proximity and spatial frequency matching between visual and tactile stimuli are necessary conditions for their interaction during binocular rivalry, while voluntary attention and action enhance the effect of touch on binocular rivalry, but are not necessary to attain the interaction.

3.2. Tactile Priming on Onset Rivalry

The survival of the effect during passive tactile stimulation rules out the possibility that voluntary action-related attention plays a critical role in mediating the interaction. We ran another experiment in which one of the two rival images was primed by a tactile cue before the onset of rivalry. Object-based attention is known to drive the first coherent percept of binocular rivalry: if a visual cue is presented before the onset of rivalry, the first dominance phase will tend to be that of the cued stimulus (Chong and Blake, 2006; Hancock and Andrews, 2007; Mitchell *et al.*, 2004). We therefore sought a similar cross-modal effect by having observers explore the tactile stimulus for 10 s in the absence of visual stimulation: as they raised the finger, the visual stimuli were displayed for 4 s, and observers had to report their first coherent percept. The average delay between the cue and presentation of the visual stimuli was 500 ms, but the separation from touch was variable according to the promptness of observers in raising their finger when instructed.

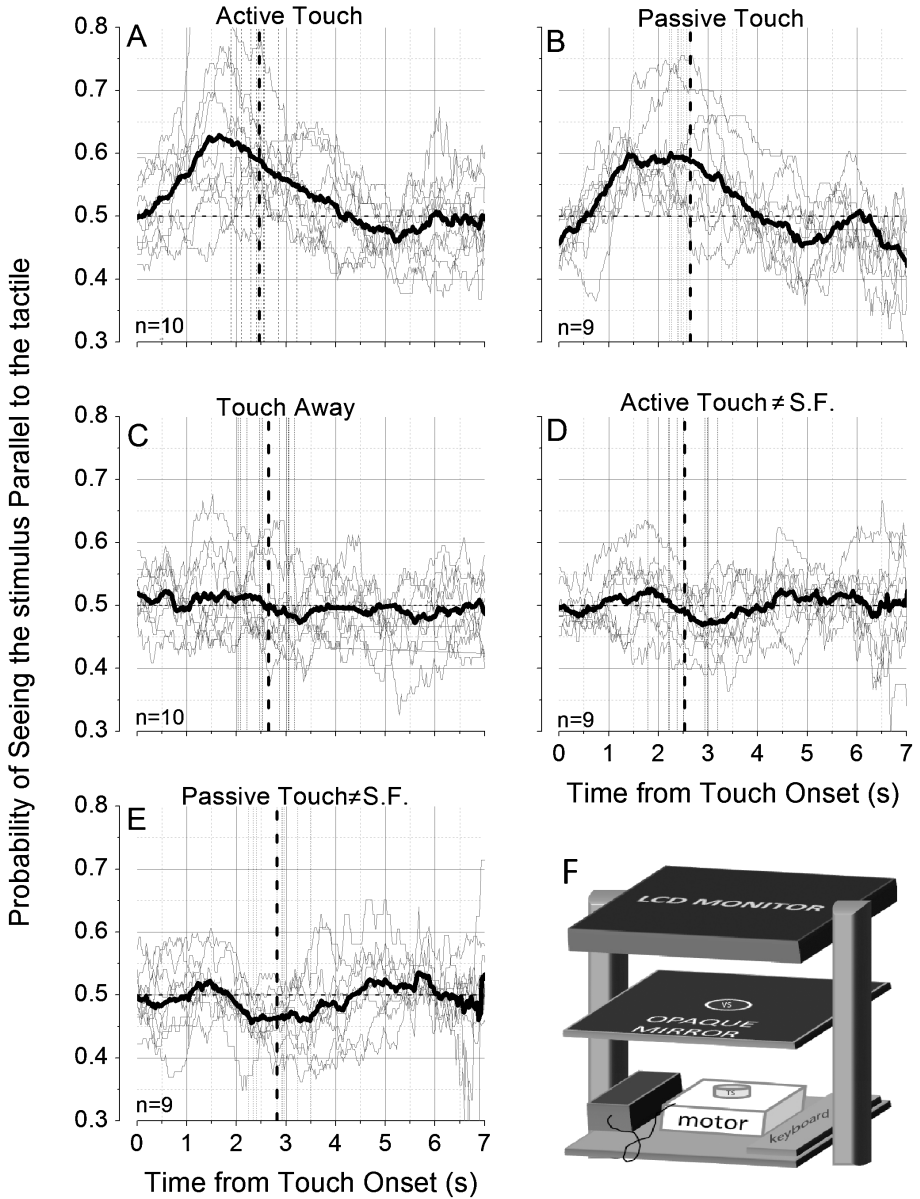
We found that the tactile cue did not bias the onset of rivalry: on average, the first coherent percept of binocular rivalry was at chance level relative to the tactile cue orientation (Fig. 3A). In our paradigm 10 s of tactile stimulation did not affect the onset of rivalry in any direction, indicating that neither tactile priming nor tactile adaptation occurred. We noticed that observers' first dominant percept remained virtually unchanged: the visual stimulus presented to their dominant eye (irrespective of orientation) dominated most of the times and the tactile cue did not affect it. We repeated the experiment shortening the duration of the tactile cue to 3 s to match the duration of touch periods during binocular rivalry, but nevertheless, tactile stimulation did not prime the onset of rivalry (Fig. 3B).

4. Discussion

The results of this study confirm previous evidence (Lunghi *et al.*, 2010) that tactile signals specifically interact with vision during binocular rivalry promoting dominance of the parallel visual stimulus, both by prolonging its dominance and by shortening its suppression. This latter result indicates that the interaction occurs outside of visual awareness, when the visual stimulus parallel to the tactile stimulus is perceptually suppressed during binocular rivalry. The relatively slow time-course of the effect of touch on the dynamics of binocular rivalry is in fact indicative of the time taken for the suppressed visual image to recover from the profound adaptation caused by binocular rivalry suppression (Alais *et al.*, 2010). The timing of the effect reflects the interaction of the tactile feedback to the visual areas with an intrinsically slow dynamics driven by adaptation and reciprocal inhibition between the monocular signals.

The most interesting result of the present study is that the effect requires spatial proximity between the visual and the tactile stimulus, suggesting that the mechanisms mediating the effect have access to a *spatiotopic* spatial map that is invariant with the sensor position. The visual and tactile objects have to be matched also in texture, pointing to a functional role of the interaction. In addition, we demonstrate that an unambiguous tactile signal can resolve binocular rivalry even when tactile stimulation is passively delivered, showing that no voluntary or cross-modal attention or action are necessary to mediate the facilitation. In the study by Lunghi *et al.*, the visual and the haptic stimuli did not overlap (the visual stimulus was presented approximately 15 cm above the haptic stimulus location) and this could be considered contradictory to the present results. However in that study, the haptic and visual stimuli were

Figure 2. Time-course of the effect. The instantaneous probability of perceiving the visual stimulus parallel to the tactile stimulus is plotted as a function of time elapsed from the onset of touch. All touch-periods are aligned at time zero. The gray thin lines are the single subject traces, while the black thick line is the average trace. The vertical dashed line represent the average duration of a touch period. The two visuo-tactile conditions (parallel and orthogonal) are collapsed together. In the Active-Touch condition (Panel 2A) the probability trace is significantly biased towards the visual stimulus parallel to the tactile stimulus 0.724 s after the onset of touch, peaks at 1.65 s and then slowly decays to chance. In the Passive-Touch condition (Panel 2B) the probability trace is significantly higher than chance 0.96 s after the onset of touch, peaks at 2.31 s and then slowly decays over time. When the visual and the tactile stimuli were in different locations (Panel 2C), or when the visual and the tactile stimuli were mismatched in Spatial Frequency (Panels 2D–E), the probability trace was flat and never significantly different from chance (*t*-test, two tailed, $\alpha = 0.025$). Panel 2F is a cartoon of the experimental setup: an opaque mirror was placed half way between the monitor and the tactile stimulus (TS), so that the visual stimulus (VS) was projected onto the TS location. Responses were collected through the keyboard. In the Passive-Touch condition, the TS was moved by a motor and tactile stimulation was delivered by the experimenter.



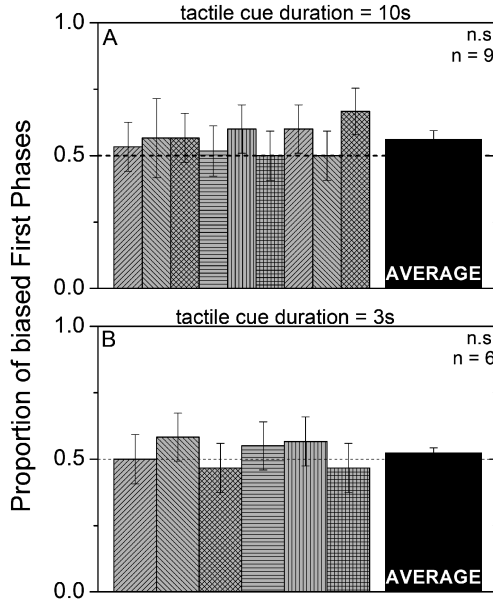


Figure 3. Tactile priming on onset rivalry. The proportion of first coherent percepts parallel to the tactile cue orientation is plotted for two conditions: in the first (Panel 3A) the duration of the tactile cue was 10 s, in the second condition (Panel 3B), the duration of the tactile cue was 3 s. The tactile cue did not prime the onset of rivalry: on average, the proportion of first dominance phases parallel to the tactile cue did not statistically differ from chance level (t -test, two tailed, $\alpha = 0.025$). The grey bars represent the single subjects' data.

vertically aligned and laid on the same plane; moreover, both the arm and the hand of the observer were stationary for the whole testing block, with only the right thumb exploring the haptic grating. In this condition the subjects had the illusory perception of touching the visual stimulus probably caused by proprioception adaptation. In the current study, when the visual and the tactile stimuli were misaligned, the observer had to actively reach the tactile stimulus by performing a voluntary action that reinforced the perception of misalignment between the visual and the tactile stimulus. Interestingly the effect reported in the current study is slightly stronger than in the previous study, reinforcing the fact that spatial alignment is important.

The unconscious, automatic nature of the effect of touch on binocular rivalry differentiates our results from the vast evidence that optimal integration between cross-sensory signals is not mandatory (Hillis *et al.*, 2002), and from previous studies on cross-sensory interactions with ambiguous visual stimuli. Auditory looming signals, when attended, can prolong the dominance phase of the visual stimulus of congruent temporal frequency during binocular rivalry, but do not curtail its suppression (van Ee *et al.*, 2009). The same is true for auditory stimuli semantically congruent with one of the visual rivaling stimuli

(a bird and a car respectively; Chen *et al.*, 2011) and for an auditory stimulus amplitude modulated at a rate matching one of the rival stimuli spatial frequency (Guzman-Martinez *et al.*, 2012).

Previous studies have shown that touch can help disambiguate visual perception: touching a rotating globe prolongs dominance of the congruent rotation direction in the kinetic depth effect (Blake *et al.*, 2004), kinesthetic information can solve the aperture problem when observers actively move a cube aligned with the visual stimulus in one of the two component directions of the visual stimulus (Hu and Knill, 2010) and touch merges with vision to improve slant discrimination (Ernst *et al.*, 2000). Fusion between visual and tactile signals during these tasks, however, is not mandatory and requires conscious perception of each of the unisensory signals. This evidence is coherent with the view that cross-modal signals are integrated at higher level associative brain areas only after being analyzed by the unisensory cortices. Our results challenge this view and are in line with a new concept that considers the whole brain as essentially multisensory (Ghazanfar and Schroeder, 2006).

Cross-modal attention modulates the activity of early visual cortices (Macaluso *et al.*, 2000) and could potentially mediate the effect that we observed. We therefore tested whether a cross-modal cue could prime the onset of rivalry. While exogenous attention has a minor effect on sustained binocular rivalry, there is evidence that an object-based attentional cue presented before the onset of rivalry can substantially bias the first coherent percept in favor of the cued stimulus (Chong and Blake, 2006; Hancock and Andrews, 2007; Mitchell *et al.*, 2004). Onset rivalry, in fact, is thought to have different properties from 'late' rivalry: it is quite stable and is susceptible to different biases (Stanley *et al.*, 2012). The intermittent presentation of the rivalry stimuli 'stabilized' binocular rivalry: an effect first described by (Leopold *et al.*, 2002) that has been attributed to perceptual memory for ambiguous figures. When primed by touch, the observers of the present study reported the same percept over several trials and touch could not disrupt this stabilization. The ineffectiveness of a tactile cue to prime the onset of rivalry suggests that simultaneous presentation of visual and tactile stimuli is a crucial factor for the interaction to occur, and rules out the possibility that the interaction between vision and touch during binocular rivalry could be entirely explained by activating attentive mechanisms with cross-modal cues. This control additionally rules out the possibility of response bias.

It has been demonstrated that voluntary action interferes with a visual signal suppressed by binocular rivalry (Maruya *et al.*, 2007), the persistence of the effect in the passive touch condition, therefore indicates that the nature of the visuo-tactile interaction is exclusively sensory. Importantly, that the effect of touch on rivalry depends on congruency of visuo-tactile spatial frequency for passive tactile stimulation further confirms that the somatosensory signal

alone is sufficient to boost the suppressed visual signal at the very first stages of visual analysis: only neurons of the primary visual cortex in fact show spatial frequency tuning as narrow as less than one octave (Maffei and Fiorentini, 1973), necessary to explain the selectivity of our effect. V1 therefore seems the prime candidate neural locus for the visuo-tactile interaction that we report. The finding that spatial proximity is necessary to fuse the visual and the tactile signals extends the specificity of the interaction: the visual and the tactile signals must be perceived as arising from the same object to be integrated. However, this also poses a problem. V1 neurons code visual space in retinotopic coordinates, while tactile information is initially coded in somatotopic space: only later at parietal levels is there evidence of mapping in visual retinotopic space (Andersen *et al.*, 1985). To explain both the spatial frequency selectivity and the spatial alignment of the two sensory maps we have to hypothesize that the interaction take place in V1, but it is mediated by a tactile signal represented in visual retinal coordinates. There is no evidence of direct projections from S1 to V1, but there is evidence of projections from STP (Falchier *et al.*, 2002) where somatosensory information may be mapped in retinotopic coordinates (Andersen *et al.*, 1985). These projections back to V1 may mediate the effect observed here.

5. Conclusions

Taken together, the results presented here suggest that the interaction between visual and tactile signals during binocular rivalry takes place at the very early stages of visual processing, probably V1. We propose that the somatosensory projections to the primary visual cortex, normally concealed by the strong and unambiguous visual signal are revealed by the temporary blindness caused by binocular rivalry suppression, and are shown in this study to be ‘retinotopically’ coded. These results bring new evidence in favor of a novel role for primary sensory cortices, which have been thought to process only unisensory information, as well as highlighting the debate about neural plasticity following sensory loss.

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