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Vestibular modulation of somatosensory perception

Elisa R. Ferrè,[1,2] Gabriella Bottini[1,3] and Patrick Haggard[2]
[1]Psychology Department, University of Pavia, Italy
[2]Institute of Cognitive Neuroscience (ICN), Alexandra House, 17 Queen Square, London WC1N 3AR, UK
[3]Cognitive Neuropsychology Laboratory, Niguarda Ca' Granda Hospital, Milan, Italy

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Abstract

Functional imaging studies show that vestibular and somatosensory projections overlap in the human brain. However, it remains unclear whether and how vestibular inputs affect somatosensory function. To address this issue, we studied the effects of left caloric vestibular stimulation (CVS) on detection of near-threshold somatosensory stimuli delivered to the left and right hands of healthy volunteers. To investigate whether these effects were somatosensory specific, or supramodal, we also tested CVS modulation of visual contrast detection. Signal detection analyses showed increased somatosensory perceptual sensitivity immediately after CVS, both ipsilaterally and contralaterally. No statistically reliable effects on visual contrast sensitivity were found. These findings suggest that vestibular stimulation has a specific facilitatory effect on somatosensory detection, distinct from non-specific arousal and spatial attentional effects of CVS. Thus, the overlap in brain activations for vestibular and somatosensory inputs is not simply an anatomical curiosity, but may reflect a functional cross-modal perceptual interaction.

Introduction

The vestibular system provides fundamental signals about the position and motion of the body, relative to the external environment. Despite the highly specialized nature of the peripheral components of the vestibular system, no exclusively vestibular cortex has been identified in either human or animal experiments. Instead, several multimodal sensory areas integrate vestibular, visual and somatosensory signals (Faugier-Grimaud & Ventre, 1989). Electrophysiological studies reported neurons responding to tactile, visual and vestibular inputs in the parieto-insular vestibular cortex (PIVC; Grüsser *et al.*, 1990a,b), the somatosensory cortex (Schwarz & Fredrickson, 1971) and the ventral intraparietal area (Bremmer *et al.*, 2002). These studies lead to the suggestion that the vestibular system may provide a basic frame of reference underpinning other sensory modalities (Angelaki & Cullen, 2008). In particular, recent functional imaging results confirmed an anatomical overlap of vestibular and somatosensory projections in healthy participants (Bottini *et al.*, 1994, 1995; Fasold *et al.*, 2002).

However, neuroimaging evidence cannot determine whether the vestibular effects on somatosensory areas are 'functionally' important. For example, the neuroimaging data are consistent with independent somatosensory and vestibular populations of neurons in the same cortical area, but not interacting. Some evidence from brain-damaged patients does suggest a functional link between vestibular and somatosensory systems. In particular, left cold caloric vestibular stimulation (CVS; Vallar *et al.*, 1990) produced a temporary remission of tactile hemianesthesia in right and left brain-damaged patients (Bottini *et al.*, 2005). However, these reports do not distinguish between direct vestibular effects on somatosensation, or indirect effects for other reasons. In particular, CVS could have only indirect effects on touch, as a consequence of its supramodal effects on spatial attention (Bisiach *et al.*, 1991).

One previous study with healthy volunteers reported an effect of vestibular stimulation on somatosensory perception. Ferrè *et al.* (2010) found that left cold CVS improved the detection of faint mechanical stimuli to the left forearm. However, this could reflect CVS-induced shifts of supramodal attention towards the left hemispace, or a general arousing effect of CVS. Therefore, it remains unclear whether CVS has a direct effect on somatosensory perception, as opposed to arousal and attention, and whether it is confined to the contralateral hemibody. Indeed, a recent study reported lasting effects of galvanic vestibular stimulation on bilateral tactile extinction (Kerkhoff *et al.*, 2011) of stimuli that were clearly suprathreshold, and that were accurately perceived during unilateral testing, suggesting an important attentional component.

To resolve these questions, we have explored vestibular–somatosensory interactions in healthy volunteers. We have used the classical left cold CVS paradigm as previous studies with hemianesthesic patients indicated that left cold CVS has the strongest somatosensory effects. The inverse paradigm, cold right CVS, did not affect somatosensory detection (Vallar *et al.*, 1993).

We improved on existing designs in several ways. First, we tested the detection of near-threshold somatosensory stimuli using signal detection analysis, to distinguish perceptual sensitivity from response bias. Second, we presented stimuli to both hands randomly and unpredictably, to control for effects of CVS on spatial attention. Third, we also tested CVS modulation of visual contrast detection in the left

Correspondence: Prof. P. Haggard, as above.
E-mail: p.haggard@ucl.ac.uk

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and right visual fields. The visual test served partly as a control for non-specific, supramodal effects of CVS, such as changes in level of arousal or spatial attention. In addition, we were interested in possible vestibular influences on visual perception given neuroimaging reports of visual cortex deactivation due to vestibular stimulation (Wenzel *et al.*, 1996; Bense *et al.*, 2001; Naito *et al.*, 2003).

Materials and methods

Participants

Twenty naïve paid participants volunteered in this experiment (mean age = 24.9 years, SD = 4.5 years). One participant was left-handed for writing. Subjects with a history of motor, somatosensory, vestibular or auditory disorders were excluded. Informed consent was obtained prior to participation in the experiment. The experimental protocol was approved by the University College London research ethics committee. The study was designed according to ethical standards of the Declaration of Helsinki.

Design and CVS procedure

Data from each participant were gathered in a single session. At the beginning of the session, participants received verbal and written instructions about the tasks. Our interest focused on specific changes in somatosensory and visual function between two experimental conditions: one before CVS (Pre-CVS condition) and one immediately after CVS (Post-CVS condition). In 10 participants, further testing 1 h after CVS (Recovery-CVS condition) was performed as a control, to check whether differences between Pre-CVS and Post-CVS conditions could reflect gradual, non-specific changes in performance, such as learning or fatigue.

CVS was performed by slowly pouring 30 mL of cold (iced) water into the external left auditory canal close to the tympanic membrane using a 50-mL syringe with a short piece of silastic tubing attached. The participant's head was positioned 30° backward from the horizontal plane, placing the lateral semicircular canal in the vertical plane, and tilted 30° toward the right. Irrigation stopped after 30 s. A plastic container placed on the subject's left shoulder was used to collect the water. CVS effectiveness was verified by the experimenter by the presence of ipsilateral slow-phase nystagmus and ipsilateral deviations in straight-ahead pointing.

A somatosensory signal detection task (SSDT) and a visual signal detection task (VSDT) were administered using a repeated-measure design with CVS condition (Pre-CVS and Post-CVS), side of stimulation (left and right hands, or left and right visual hemifields) and stimulus type (below and above threshold) as within-subject variables. Task order was counterbalanced between subjects. Because CVS effects have a limited duration, care was taken to ensure both tasks were completed within 15 min following CVS, which corresponds to the window of maximal effect (Bárány, 1906; Bottini *et al.*, 1995; Ngo *et al.*, 2007).

SSDT

Stimuli were delivered via 4-mm-diameter concentric electrodes (Tursky *et al.*, 1965) attached to right or left middle fingertips by surgical tape. Stimulation was provided by a custom-built electrical stimulator, whose current level and pulse duration were controlled by a computer. Within the range used here, shock intensity depends only on the total charge transferred from the electrode, which is the product of current pulse amplitude and pulse duration. Therefore, we obtained estimates of somatosensory perception by holding pulse amplitude at 10 mA and varying pulse duration (cf. Voss *et al.*, 2006). We first used standard staircase procedures (Levitt, 1971) to estimate the lowest shock intensity at which exactly five of 10 stimuli were detected. To initially calibrate shock intensity for each participant, the pulse width was started at 20 μs and increased in steps of 10 μs until the participant reported the presence of the stimulus. If the participant did not detect the stimulus the shock intensity was increased. If the participant responded 'yes' three times consecutively, the pulse width was reduced by 5 μs. Progressively smaller changes in intensity were applied to the stimulus until the participant was able to detect it. This level was averaged across three successive staircases to estimate somatosensory threshold.

The experimental SSDT consisted of five trial types: 30 trials clearly above threshold (+10%) on the left and 30 on the right fingers, 30 trials slightly below threshold (−10%) on the left and 30 on the right fingers. We also presented a further 30 catch trials, in which no signal was present. Trial order was randomized, so that participants could not predict stimulus presence, stimulus intensity or the finger stimulated. Participants were blindfolded throughout the task. The beginning of each trial was signalled by two auditory beeps. The shock, if present, was delivered after a variable interval of between 500 and 750 ms. One-hundred milliseconds later, a beep of a different frequency indicated the end of the trial. Participants made unspeeded verbal responses ('yes'/'no'). They were only required to indicate whether or not they felt the tactile stimulus, and did not report which finger was stimulated. The overall duration of the SSDT was about 5 min. Data for each trial were recorded and analysed later.

VSDT

The VSDT was designed to have similar characteristics to SSDT. The Freiburg visual acuity test (Bach, 1996) was used to identify the Michelson fraction for visual contrast threshold perception. Participants sat 100 cm from a 15″ computer screen (screen resolution 1280 × 800). Stimuli were Landolt-like C optotypes, appearing 1° of visual field left or right of a central fixation point, in randomized sequence, and at random inter-trial intervals. Participants were instructed to detect the presence of the optotype, pressing a left key if they detected the stimulus and a right key otherwise. The overall duration of the VSDT was about 5 min. The following trials were delivered in random order: 30 trials above (+10%) and 30 below contrast threshold (−10%) in the left hemifield, 30 trials above (+10%) and 30 below contrast threshold (−10%) in the right hemifield. Thirty catch trials were randomly interspersed. Data were recorded and analysed later.

In both SSDT and VSDT, our interest focussed on detection of faint tactile and visual stimuli. Stimuli that were clearly perceptible (+10% above-threshold trials) were included as a reminder of the quality of the stimulus, so that the participants had a clear representation of the stimulus that they were trying to detect. We did not predict these strong stimuli would be affected by CVS (Ferrè *et al.*, 2010).

Data analysis

SSDT and VSDT results were analysed using signal detection analysis (Macmillan & Creelman, 1991). We considered the number of hits (number of stimulus-present trials in which participants said 'yes'), false alarms (number of stimulus-absent catch trials in which participants said 'yes'), misses (number of stimulus-present trials in

which participants said 'no') and correct rejections (number of stimulus-absent catch trials in which participants said 'no').

Hit rates [P('yes'|stimulus present), proportion of hit trials to which subject responded 'yes'] and false alarm rates [P('yes'|stimulus not present), proportion of trials in which there is not actually the stimulus to which subject responded 'yes'] were calculated. These were used to obtain the perceptual sensitivity (a'), a measure of discriminability in detecting the signal against background noise; a' does not require homogeneous variance and it can be calculated even if the hit or false alarm rates are 1 or 0. The tendency to report stimuli as present (C, response bias) was also obtained. Sensitivity and response bias were calculated for each CVS condition, and each side of stimulation.

Results

CVS effectiveness

Although CVS is mildly unpleasant, no participant reported experiencing any particular discomfort and no participant withdrew from the study. All participants showed clear ipsilateral slow-phase of nystagmus immediately after left CVS, as verified by the experimenter. Pointing straight-ahead results showed a significant leftward bias in the Post-CVS condition compared with the Pre-CVS condition (Table 1). The effect of CVS on pointing error was highly significant ($t_{19} = 5.704$, $P < 0.0001$). This demonstrates the effectiveness of our caloric vestibular stimulation, according to established criteria (Karnath *et al.*, 2003).

Effects of CVS on sensitivity and response bias for each sensory modality

Our main interest lay in the effects of CVS on detection of near-threshold stimuli. The average tactile detection rate for near-threshold stimuli on both hands was 24.7% in the Pre-CVS condition, rising to 46% in the Post-CVS condition. The average visual detection rate for below-threshold stimuli for both hemifields was 36.7% in the Pre-CVS condition, rising to 43.2% in the Post-CVS condition (Table 2).

TABLE 1. Pointing straight-ahead results

	Pre-CVS (mm)	Post-CVS (mm)
s1	−12	−26
s2	56	25
s3	6	−6
s4	−1	−65
s5	−2	−30
s6	67	23
s7	−11	−29
s8	−2	−50
s9	15	−142
s10	12	−34
s11	21	−79
s12	25	−43
s13	14	−98
s14	13	2
s15	−12	−33
s16	46	24
s17	−2	−22
s18	12	−16
s19	41	−27
s20	13	−63
Mean	14.95	−34.45
SD	22.39	41.49

Pointing straight-ahead results in each condition (mm). Negative values indicate a leftward displacement and positive values a rightward displacement. Note the strong leftward bias in the Post-CVS condition. CVS, caloric vestibular stimulation.

SSDT and VSDT estimates of perceptual sensitivity (a') and response bias (C) were analysed using 2 × 2 univariate ANOVAs with factors of CVS Condition (Pre-CVS vs. Post-CVS) and Side (Left vs. Right). Analysis of SSDT sensitivity (a') showed a significant effect of CVS Condition ($F_{1,19} = 11.381$, $P = 0.003$, effect size – Cohen's $d = 0.98$). There was no effect of Side ($F_{1,19} = 1.999$, $P = 0.174$). We note that the same false alarm rate was used for both Left and Right, so the a' values for Left and Right are not fully independent, as they both include this common term. The interaction between CVS Condition and Side was also not significant ($F_{1,19} = 1.603$, $P = 0.221$). A similar ANOVA applied to the a' data in the VSDT showed no significant effect of CVS Condition ($F_{1,19} = 0.009$, $P = 0.924$), no effect of Side ($F_{1,19} = 0.825$, $P = 0.375$), and no interaction between CVS Condition and Side ($F_{1,19} = 1.441$, $P = 0.245$; Fig. 1).

Analyses of response bias (C) showed that CVS slightly increased the bias to report a stimulus as present, particularly on the left side. SSDT C-values showed a significant effect of CVS Condition ($F_{1,19} = 5.573$, $P = 0.027$; effect size – Cohen's $d = 0.59$), no main effect of Side ($F_{1,19} = 1.455$, $P = 0.243$), and an interaction between CVS Condition and Side ($F_{1,19} = 7.311$, $P = 0.014$). We used simple effects analysis to explore this interaction, holding the level of each factor constant and investigating the effects of the other factor. Thus, there was a significant difference between Pre-CVS and Post-CVS conditions ($t_{19} = 2.883$, $P = 0.010$) for the left hand, but not for the right hand ($t_{19} = 1.719$, $P = 0.102$). Further, we found a significant difference between the left and right hands in the Pre-CVS condition ($t_{19} = 2.382$, $P = 0.028$), but not for the Post-CVS condition ($t_{19} = 0.116$, $P = 0.909$). For VSDT response bias, there was no effect of CVS Condition ($F_{1,19} = 0.775$, $P = 0.390$), no effect of Side ($F_{1,19} = 0.383$, $P = 0.544$), and no interaction between CVS Condition and Side ($F_{1,19} = 2.484$, $P = 0.132$; Fig. 2).

For completeness, we also analysed the effect of CVS on perception of stimuli above threshold. These stimuli were included in our experimental design to remind participants of the stimuli to be detected, rather than to test any experimental hypotheses. In the Pre-CVS condition the average tactile detection of above-threshold stimuli for both hands was 76.1%, condition compared with 77.6% in the Post-CVS condition. Interestingly, visual detection of above-threshold stimuli for both hemifields was much better than for somatosensory stimuli, although both stimuli were at the same level relative to threshold – 92.1% Pre-CVS condition compared with 94.4% Post-CVS condition. A 2 × 2 ANOVA with factors of CVS Condition (Pre-CVS vs. Post-CVS) and Side (Left vs. Right) was applied to a' and C data for above-threshold stimuli on each task. As predicted, analysis of sensitivity (a′) showed no significant main effect of CVS Condition ($F_{1,19} = 0.283$, $P = 0.601$), Side ($F_{1,19} = 0.007$, $P = 0.993$), or interaction between CVS Condition and Side ($F_{1,19} = 0.134$, $P = 0.718$). For the a' data in the VSDT, we found no main effect of CVS Condition ($F_{1,19} = 0.029$, $P = 0.867$), but trends towards a main effect of Side ($F_{1,19} = 3.797$, $P = 0.066$) and towards an interaction between CVS Condition and Side ($F_{1,19} = 3.353$, $P = 0.083$). In summary, the CVS-induced increase in SSDT sensitivity found for near-threshold stimuli was not observed for above-threshold stimuli. This finding extends an earlier previous report of accuracy rates in detecting unilateral mechanical stimuli near vs. above threshold (Ferrè *et al.*, 2010).

Analyses of response bias (C) showed that CVS slightly increased the bias to report a suprathreshold stimulus as present on the right side. SSDT data showed no main effect of CVS Condition ($F_{1,19} = 1.638$,

TABLE 2. Hit rates and false alarm rates results

	SSDT			VSDT		
	Hits (%)			Hits (%)		
	L	R	False alarms (%)	L	R	False alarms (%)
Pre-CVS	18.83 (3.21)	30.5 (4.47)	5.67 (2.07)	33.17 (7.03)	40.17 (7.78)	7.17 (2.31)
Post-CVS	42.83 (4.39)	49.17 (6.83)	5.17 (1.68)	41.83 (7.19)	44.5 (7.85)	10.83 (2.96)

Means (and standard errors) of hit rates and false alarm rates in Pre-CVS and Post-CVS conditions. CVS, caloric vestibular stimulation; SSDT, somatosensory signal detection task; VSDT, visual signal detection task.

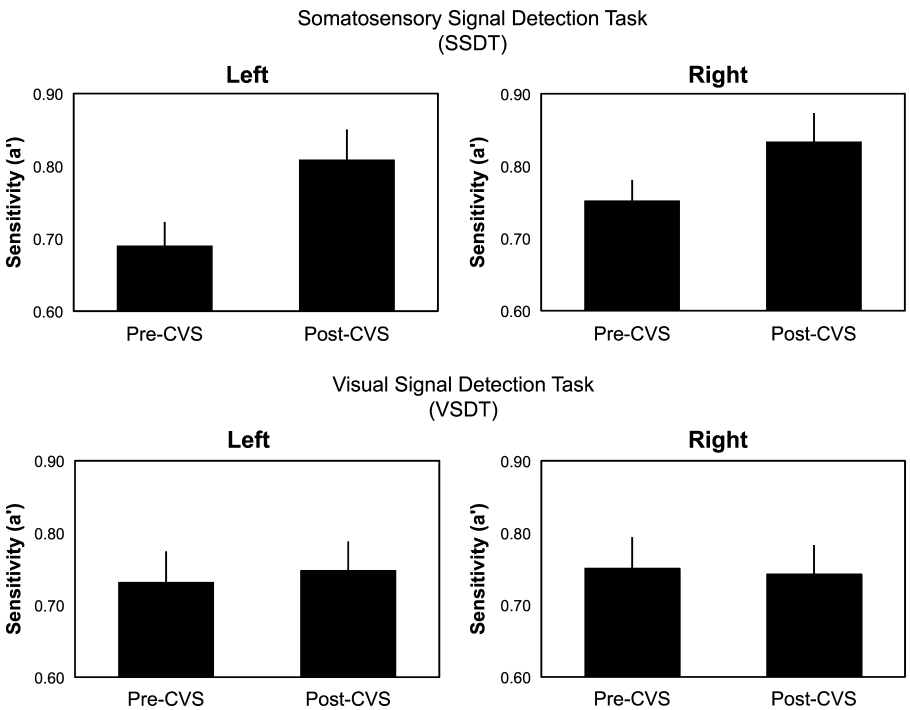

FIG. 1. Sensitivity results. Perceptual sensitivity (a') values as a function of each condition (error bars indicate SEM). Note the improvement in sensitivity bilaterally in the somatosensory signal detection task (SSDT), while no effects on the visual signal detection task (VSDT) data. CVS, caloric vestibular stimulation.

$P = 0.216$), no main effect of Side ($F_{1,19} = 0.531$, $P = 0.475$), and a significant interaction between CVS Condition and Side ($F_{1,19} = 4.509$, $P = 0.047$). *Post hoc* comparisons showed a marginally significant difference between Pre-CVS and Post-CVS conditions on the right side ($t_{19} = 2.111$, $P = 0.048$), but not for the left side ($t_{19} = 0.160$, $P = 0.874$). Further, we found no significant differences between the left and right hands in the Pre-CVS condition ($t_{19} = -7.06$, $P = 0.488$), or for the Post-CVS condition ($t_{19} = 1.485$, $P = 0.154$). A similar ANOVA applied to the *C*-data in the VSDT showed a significant main effect of Side ($F_{1,19} = 12.757$, $P = 0.002$, effect size – Cohen's $d = 0.16$) and a trend towards a main effect of CVS condition ($F_{1,19} = 3.797$, $P = 0.066$), but no interaction ($F_{1,19} = 0.042$, $P = 0.839$).

Effects of CVS comparisons across sensory modalities

Neuroimaging studies demonstrated that vestibular stimulations affected in different directions somatosensory and visual systems, enhancing the neuronal activity in the first case (Bottini *et al.*, 1995) and causing deactivations in the second case (Bense *et al.*, 2001). To compare CVS effects across somatosensory and visual modalities we used two distinct analysis approaches. First, SSDT and VSDT estimates of a' and C were analysed using 2×2 univariate ANOVAs with factors of CVS Condition (Pre-CVS and Post-CVS) and Modality (Somatosensory and Visual). Analysis of sensitivity showed no effect of CVS Condition ($F_{1,19} = 3.424$, $P = 0.08$) and no effect of Modality ($F_{1,19} = 4.414$, $P = 0.528$), but an interaction between these effects that approached the conventional boundary of significance ($F_{1,19} = 3.717$, $P = 0.068$). This arose because the two modalities had similar sensitivities in the Pre-CVS condition ($t_{19} = -0.387$, $P = 0.703$), but somatosensory sensitivity was selectively enhanced Post-CVS condition ($t_{19} = 6.260$, $P < 0.0001$).

Analyses of response bias (C) showed a marginally significant main effect of CVS Condition ($F_{1,19} = 4.426$, $P = 0.049$), no main effect of Modality ($F_{1,19} = 1.396$, $P = 0.252$) and an interaction between CVS Condition and Modality, which again approached the conventional boundary of significance ($F_{1,19} = 4.061$, $P = 0.058$).

Our second analysis addressed the question – which modality is more affected by CVS, vision or somatosensation? To do this, we used a multivariate approach, treating our a' and C measures as multiple

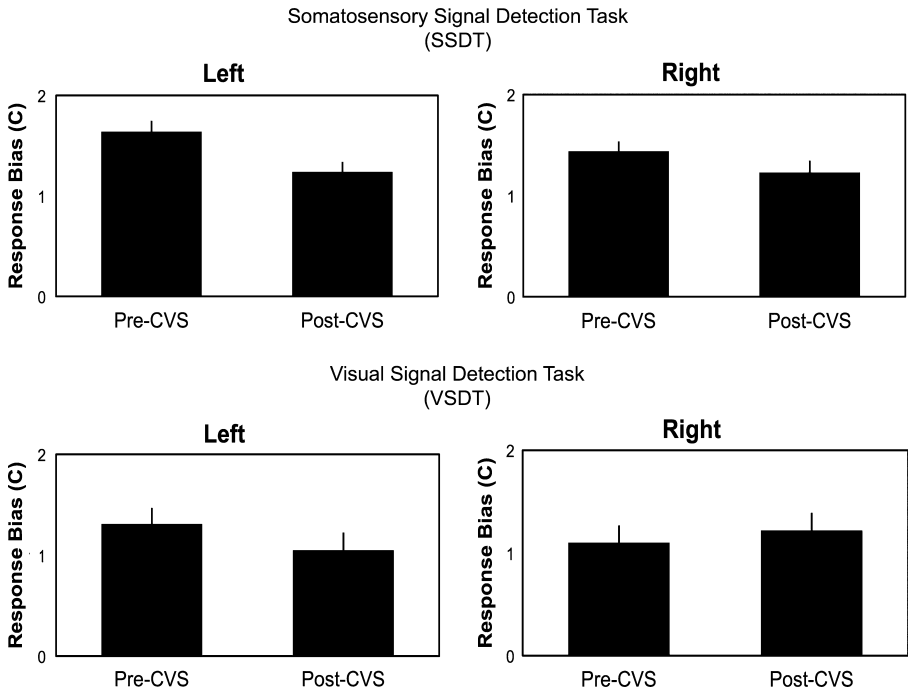

FIG. 2. Response bias results. Response bias (C) values as a function of each condition (error bars indicate SEM). After vestibular stimulation the response bias became more liberal in the somatosensory signal detection task (SSDT), while no effects on the visual signal detection task (VSDT) data. CVS, caloric vestibular stimulation.

dependent variables in a single analysis. Visual and somatosensory performance may be more appropriately considered as separate dependent variables measuring different outputs of a neural system, rather than different levels of an independent input variable manipulated by an experimenter. Moreover, sensitivity and bias are clearly different dependent variables, by the assumptions of signal detection theory. Therefore, we applied multivariate analysis of variance (MANOVA), treating a' and C in SSDT and VSDT as four simultaneous dependent variables. CVS Condition (Pre-CVS and Post-CVS) and Side (Left and Right) were used as factors. We again found a significant main effect for CVS Condition, Wilks' $\lambda = 0.284$, approximated by $F_{4,15} = 9.41$, $P = 0.0005$. Inspection of standardized canonical coefficients showed that this difference arose primarily from SSDT sensitivity (a' coefficient 1.181), with a contribution from the SSDT bias (C coefficient −0.99). In contrast, coefficients for VSDT sensitivity (a' coefficient 0.31) and VSDT bias (C coefficient −0.42) were negligible. Comparing these coefficients provides a direct 'numerical' comparison of CVS effects across modalities – modulation of somatosensory sensitivity was 3.80 times greater than modulation of visual sensitivity. To provide a 'statistical' comparison, we performed 1000 permutations, randomly exchanging Pre-CVS condition and Post-CVS condition data. Only 51 of these 1000 permutations (5.1%) contained imbalances between SSDT and VSDT sensitivity coefficients that were as great as the 3.80 ratio found in our data. Note that this permutation test considered only the imbalance between modality sensitivity coefficients, irrespective of the direction, size and significance of the difference between permuted Pre-CVS condition and Post-CVS condition data. The permutation tests suggest that the CVS effects in our actual data were not only statistically reliable in themselves, but were also distributed 'across' modalities in a highly specific manner that was unlikely to have arisen by chance. Finally, no multivariate effects of Side (Left and Right) and no interaction between CVS Condition and Side were found ($P > 0.05$).

Possible effects of task difficulty

To test whether our results might be sensitive to task difficulties across somatosensory and visual tasks, we directly compared a' data of the different modalities in our baseline condition before vestibular stimulation (Pre-CVS condition). Comparisons between SSDT sensitivity and VSDT a' data showed no significant difference in both left ($t_{19} = -0.693$, $P = 0.496$) and right side ($t_{19} = 0.020$, $P = 0.984$).

Possible learning/fatigue effects

To investigate whether our tasks might be sensitive to overall learning or fatigue effects, we compared the performance of the first ten participants between the Pre-CVS and the Recovery-CVS conditions. We performed a 2 (CVS Condition – Pre-CVS vs. Recovery-CVS) by 2 (Side – Left vs. Right) univariate ANOVA design on SSDT data. No effect of CVS Condition ($F_{1,9} = 0.376$, $P = 0.555$), no effect of Side ($F_{1,9} = 0.115$, $P = 0.742$), and no interaction between CVS Condition and Side ($F_{1,9} = 1.577$, $P = 0.241$) were found in SSDT sensitivity (a').

Analysis of response bias (C) showed no significant effect of CVS Condition ($F_{1,9} = 0.306$, $P = 0.594$), no effect of Side ($F_{1,9} = 1.512$, $P = 0.250$), and no interaction between CVS Condition and Side ($F_{1,9} = 0.690$, $P = 0.428$). Similar results emerged when analysing VSDT sensitivity (a') and response bias (C) (all $P > 0.05$; Table 3).

Discussion

This study investigated the functional effect of vestibular stimulation on somatosensory detection. A visual contrast sensitivity task was used to control for non-specific, supramodal effects, such as arousal and shifts of attention. The most striking result was a clear, positive modulation of CVS on perceptual sensitivity in a somatosensory detection task. That is, vestibular stimulation made participants more

TABLE 3. Learning/fatigue effect

	SSDT		VSDT	
	Left	Right	Left	Right
Sensitivity (a')				
Pre-CVS	0.65 (0.06)	0.73 (0.06)	0.69 (0.07)	0.72 (0.08)
Recovery-CVS	0.67 (0.03)	0.62 (0.09)	0.61 (0.14)	0.67 (0.09)
Response bias (C)				
Pre-CVS	1.49 (0.19)	1.26 (0.16)	1.33 (0.26)	1.22 (0.26)
Recovery-CVS	1.54 (0.27)	1.47 (0.28)	0.85 (0.31)	0.75 (0.29)

Mean a'- and C-values (and standard errors) for the experimental conditions in which the vestibular stimulation is not present (Pre-CVS and Recovery-CVS). No significant differences are present for both sensitivity and response bias. CVS, caloric vestibular stimulation; SSDT, somatosensory signal detection task; VSDT, visual signal detection task.

sensitive in detecting somatosensory stimuli. The vestibular–somatosensory enhancement was found for detection of shocks on both left and right hands, i.e. both ipsilateral and contralateral to our left cold CVS.

CVS also induced some changes in the response bias, making participants more liberal in responding 'yes' after vestibular stimulation. However, these changes were not ubiquitous. For the SSDT, they were concentrated on the left hand. This could possibly reflect a spatial attentional effect of CVS (Vallar *et al.*, 1990; Bisiach *et al.*, 1991). However, the attentional account cannot readily explain why the bias was reversed for suprathreshold stimuli, where we found a liberal bias for the right hand. Further, our signal detection approach allowed us to estimate changes in sensitivity independent of response bias. Moreover, multivariate analysis showed that effects of CVS on sensitivity were stronger than those on bias. No effects on visual contrast sensitivity or bias were found. We also excluded interpretations based on task difficulty or learning/fatigue through additional analyses.

Although CVS has strong effects on spatial attention in right brain-damaged patients (Rubens, 1985), Rorden *et al.* (2001) found that CVS did not modulate covert visual attention in healthy volunteers. Our data confirm this result. First, we found no evidence for side-specific modulation of somatosensory sensitivity. Second, our specific bilateral effect of CVS on somatosensory detection cannot easily be explained by a modulation of spatial attention. Based on the neuropsychological evidence, simple orientation of attention toward the left hemispace would have produced lower detection thresholds on the left hand, but not on the right hand, and lower visual contrast threshold in left but not in right hemifield; nor can our results be ascribed to a vestibular induced modulation of general arousal as CVS selectively affected somatosensory detection but not visual detection. Thus, we conclude that vestibular–somatosensory links have important perceptual consequences, and are not restricted to the neuroanatomical overlap or co-location of brain activations seen in neuroimaging studies, nor do they result from vestibular driving of a supramodal attentional system (Macaluso & Driver, 2005). Rather, vestibular–somatosensory links involve a specific cross-modal perceptual enhancement (Stein & Meredith, 1993).

Vestibular stimulation can change high-level somatosensory representations and bodily awareness – a dramatic transient recovery of tactile extinction (Vallar *et al.*, 1990), somatoparaphrenia (Bisiach *et al.*, 1991) and anosognosia (Cappa *et al.*, 1987) are observed in right brain-damaged patients immediately after vestibular stimulation. Furthermore, CVS may induce temporary remission of phantom limb sensation in amputees (André *et al.*, 2001) and paraplegic patients (Le Chapelain *et al.*, 2001). Therefore, the effects of CVS appear to be wide-ranging. However, to our knowledge, ours is the first investigation of vestibular influences on low-level perceptual functions in different modalities, using the same participants and comparable psychophysical tasks. A few previous studies have investigated effects of CVS on visual perception as distinct from visuospatial attention. CVS was reported to modulate binocular rivalry (Miller *et al.*, 2000), although the lateralized pattern of the effect suggests this result includes an attentional component. Interestingly, Bense *et al.* (2001) showed that vestibular stimulation bilaterally deactivated the occipital visual cortex (BA 17–19). This result is difficult to reconcile with a general alerting or attentional hypothesis of vestibular stimulation. The combination of somatosensory activations and visual deactivations in neuroimaging provided us with a motivation to compare effects of CVS on touch and vision. Because CVS influences eye movements, notably the slow phase of nystagmus, several precautions are required when combining vestibular stimulation and visual psychophysics. We therefore used experimental procedures from previous studies that directly tested effects of CVS on vision (Miller *et al.*, 2000; Ngo *et al.*, 2007, 2008). First, the visual and somatosensory tasks were not administered during CVS itself, but a few minutes after irrigation. At this time, no signs of ongoing nystagmus or vertigo were present. Moreover, the visual task was performed during central fixation. In contrast, the nystagmus that immediately follows CVS is found predominantly during peripheral fixation ipsilateral to the stimulated ear. Therefore, we consider it unlikely that our visual measures were affected by oculomotor effects of CVS. Interestingly, we did not find

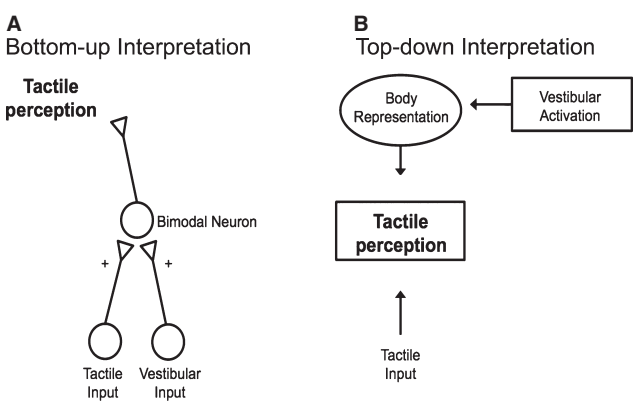

FIG. 3. Vestibular modulation of somatosensation. (A) Vestibular and somatosensory information converge on bimodal neuron in a feedforward fashion directly enhancing tactile perception. (B) Vestibular input provides a top-down modulation of somatosensory cortical areas that improves tactile perception.

any reliable evidence of visual impairment following CVS, contrary to the prediction from neuroimaging studies showing deactivation of primary visual areas – further research may be required to investigate whether vestibular inputs have direct, functional effects on visual perception. For the moment, our finding of enhanced somatosensory sensitivity without changes of visual sensitivity suggests a modality-specificity modulation induced by CVS.

We found CVS-induced improvement in somatosensory perception not only ipsilateral but also contralateral to vestibular stimulation. After left CVS, somatosensory detection was improved on both the left and right hand. This bilateral effect could be explained in at least two ways. First, left CVS primarily stimulates the right hemisphere, and the right hemisphere may contain representations of both the left and right hemibody (Bottini *et al.*, 2005). Alternatively, CVS may influence somatosensory areas that have strong transcallosal connections, and/or bilateral receptive fields, such as the secondary somatosensory cortex (SII; Iwamura *et al.*, 1994). Although detection was thought to occur in the more lateralized primary somatosensory cortex (SI), rather than the more bilateral SII (Lin & Forss, 2002), recent neuroimaging studies demonstrated that faint stimuli delivered on the hand activated both contralateral SI cortex and SII cortex bilaterally (Blankenburg *et al.*, 2003).

Two alternative mechanisms could explain these effects. First, a bottom-up interpretation can explain our data by vestibular and somatosensory information convergence on bimodal neurons in a feedforward fashion (Odkvist *et al.*, 1974; Fig. 3A). Electrophysiological studies identified convergence of vestibular and somatosensory signals in some PIVC neurons (Grüsser *et al.*, 1990a,b). Moreover, most PIVC neurons have a tactile receptive field mainly responding to stimulation of the neck region of the primate (Grüsser *et al.*, 1990a,b). The convergence of vestibular and somatosensory inputs emphasizes a functional multimodal interaction useful for coding the body in the environment. This model assumes that somatosensory detection is not purely unimodal, but that bimodal neurons that integrate both somatosensory and vestibular input contribute to detection. The bottom-up interpretation would suggest that such neurons should respond to vestibular and somatosensory inputs, which occur 'simultaneously', or in close temporal synchrony (e.g. Kornhuber, 1965; Avillac *et al.*, 2007). However, CVS has poor temporal specificity and does not allow the role of temporal synchrony to be tested in detail.

Alternatively, vestibular input could provide a top-down modulation of somatosensory cortical areas (Fig. 3B). For example, vestibular stimulation might boost somatosensory processes by providing intrinsic information about the body (Bottini *et al.*, 1995), while downregulating the visual system by the reciprocal inhibitory visual–vestibular interactions (Brandt *et al.*, 1998). This vestibular rebalancing of somatosensory systems might prioritize key somatosensory functions when the normal relation of the organism to its environment is altered. In keeping with this suggestion, Arzy *et al.* (2006) found that stimulation of a key vestibular multisensory area in the right temporoparietal junction provoked both out of body experiences and distortions of intrinsic somatosensation. Moreover, the top-down model suggests that effects of CVS on tactile perception could be just one instance of a more general vestibular mechanism modulating the interaction between the body and the external environment. For example, head posture modulates the perception of virtual head rotation caused by galvanic vestibular stimulation. Head posture does not affect which vestibular canals are stimulated, but alters how the vestibular signal is coded in egocentric coordinates or in an external frame of reference (Day & Fitzpatrick, 2005). Thus, the vestibular signal is constantly computed to give information about the whole body in space.

To conclude, we have shown that left cold CVS improves somatosensory detection bilaterally in healthy participants. These effects are specific to somatosensation, and do not simply reflect general visuospatial attention. The vestibular system may determine a cortical division of labour between intrinsic body representation and representation of the external environment.

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Abbreviations

CVS, caloric vestibular stimulation; PIVC, parieto-insular vestibular cortex; SI, primary somatosensory cortex; SII, secondary somatosensory cortex; SSDT, somatosensory signal detection task; VSDT, visual signal detection task.

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