RESEARCH ARTICLE

Juggling reveals a decisional component to tactile suppression

Georgiana Juravle · Charles Spence

Abstract Goal-directed movements are characterized by sensory suppression, that is, by decreased sensitivity to tactile stimuli. In the present study, we investigated tactile suppression during movement using a complex motor task: basic 3-ball juggling. It was hypothesized that a decrease in tactile sensitivity would be observed, together with a shift in participants' response bias while juggling. In a first experiment, participants had to detect a short gap in an otherwise continuous vibratory stimulus, which was delivered to their wrist under conditions of rest or else while juggling. In a second experiment, participants detected a short time gap in a continuous auditory signal, under the same conditions. In a final control experiment performed at rest, participants detected a short time gap in an auditory or tactile signal. In an additional condition, the detection of a gap in tactile stimulation was required under conditions of intramodal tactile interference. Participants were significantly less sensitive to detect a gap in tactile stimulation whilst juggling. Most importantly, these results were paired with a significant shift toward participants adopting a more conservative criterion when responding to the presence of the gap (i.e. they were more likely to say that a gap was not present). Taken together, these results demonstrate movement-related tactile sensory suppression and point to a decisional component in tactile suppression, thus suggesting that tactile suppression could already be triggered in the brain ahead of the motor command.

Introduction

In our everyday life, we interact with the surrounding environment by means of goal-directed movements: we make eye movements to objects of interest, and we reach for, and grasp, objects in order to manipulate them as a function of our current goals. However, the execution of goal-directed movements can sometimes be interfered with by stimuli that happen to be presented in other sensory modalities (Brozzoli et al. 2009) or by the performance of other concurrent tasks (Gallace et al. 2010).

Recently, it has been demonstrated that tactile discrimination performance is impaired during simple goal-directed reach-to-grasp movements (Juravle et al. 2010). The participants in Juravle et al.'s study had to perform a dual-task with a speeded movement task and a non-speeded perceptual task. In each trial in the movement task, the participants prepared and executed a speeded reach-to-grasp movement, following an auditory go signal. In the perceptual task, a tactile standard pulse was presented to the participant's left hand, which was kept at rest throughout the trial. Their mobile right hand received a second test pulse, which could be delivered, depending on the experimental condition, in the motor preparation period, in the early, middle and late execution periods, or in the post-movement period. The participants had to judge whether the intensity of the second pulse delivered to the moving hand was either stronger or weaker than the pulse delivered to the resting hand. The results revealed significant changes in tactile sensitivity, with lower thresholds (i.e. better performance) in the motor preparation and post-movement periods, and significantly

G. Juravle (✉) · C. Spence
Crossmodal Research Laboratory,
Department of Experimental Psychology, Oxford University,
South Parks Road, Oxford OX1 3UD, UK
e-mail: georgiana.juravle@psy.ox.ac.uk

higher tactile discrimination thresholds (i.e. poorer performance) in the movement execution period. The significantly increased tactile thresholds measured over the movement execution period demonstrate that tactile perception deteriorates while our limbs are in motion, a phenomenon known as sensory suppression or attenuation (Chapman and Beauchamp 2006; Voss et al. 2006).

This tactile suppression, occurring during movement execution, is commonly attributed to a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Chapman and Beauchamp 2006). Forward models of motor control posit an internal representation of the body and of the signals from the environment that are used to predict the consequences of the outgoing motor command (Miall and Wolpert 1996; Wolpert et al. 1995). One of the main roles of internal models in movement control is to regulate performance by comparing the predicted sensory states with the actual ones. Moreover, forward models are used to attenuate unnecessary sensory information and enhance the essential sensory information for movement control (i.e. sensory cancellation from the movement or reafference). It has been suggested that by attenuating the sensory signals resulting from the movement, such a predictive mechanism serves to enhance the salience of external events or those that cannot be predicted from the motor command (Bays and Wolpert 2007).

In the present study, we investigated tactile suppression in a complex, practiced bimanual task, i.e., juggling. For this, we used the power of signal detection theory (SDT, Green and Swets 1966; Macmillan and Creelman 2005) to derive measures of sensitivity, together with response bias in the tactile domain, under conditions of rest and movement. Sensitivity (d') provides a measure of the true separation between signal (i.e. gap present in tactile stimulation, as in the present study) and noise (i.e. gap absent). Sensitivity, therefore, reflects the characteristics of the stimulus and is independent of response bias. In this respect, the better the separation between signal and noise, the more sensitive a participant will be. Response bias, on the other hand, is characteristic to the participant: In a YES/NO task, such as in the experiments reported in the present study, participants will likely favour one response or the other. SDT allows one to identify the criterion location (criterion c) in the decision space. Its distribution is centred at zero, and extreme values are given by either very small or very large amounts of true positive responses (TP, i.e., a YES response when a target was present) or false positive responses (FP, i.e., a YES response when the target was absent). Given that zero constitutes the unbiased location, positive values of the criterion c indicate a tendency toward saying 'NO', whereas negative values indicate the tendency to say 'YES'. Moreover, another measure of response bias offered by SDT is the relative criterion location c', measure derived by scaling the criterion location to the measured sensitivity. If c is independent of sensitivity, c' is clearly influenced by sensitivity. When d' varies across conditions, the relative criterion c' is a good measure of the strength of the criterion needed in order to obtain a certain amount of bias (see Macmillan and Creelman 2005, for a discussion of the usefulness of the different criteria).

The participants in our first experiment had to detect a short gap in an otherwise continuous tactile vibration under conditions of no movement (rest) and juggling. The juggling task was chosen as it seemed to provide a means of exploring the dynamics of tactile perception, our central concern. Therefore, as a first step, we were interested to investigate whether a differential pattern of sensitivity would be observed for the successive 'catches' and 'throws' of the balls occurring during the hand movements used while juggling. Another exploratory hypothesis was related to the timing of the juggling activity: We were interested to investigate whether the exact point in time during the trial when the target (i.e. the short time gap) is presented (whether the beginning of the movement, the middle or the end point) makes a difference with respect to participants' sensitivity to it. Lastly, taking into consideration the sensory suppression experienced during movement, we hypothesized that participants would be more sensitive to gaps in tactile stimulation when their hands were at rest, as compared to the juggling condition in which a significant deterioration in participants' tactile perception was expected. At the same time, given the 'tactile uncertainty' favoured by the movement of both hands, a differential pattern in both criteria c and c' was expected during the active juggling phase, as opposed to the rest condition.

Experiment 1

Participants

Ten jugglers (6 male, one left handed) took part in this experiment (mean age of 24 years; age range 20–30 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. The participants had been juggling for approximately 8 years on average (ranging from 3 to 20 years). All of the participants were comfortable with basic 3-ball juggling. The experimental session lasted for approximately 75 min, and the participants received a £10 (British pounds) gift voucher in return for taking part in the study.

Apparatus

The experiment took place in a 1.6-m wide corridor. Illumination was provided by several ceiling lights. The participants had one tactor (VBW32 skin stimulator, 1.6 × 2.4 cm vibrating surface, Audiological Engineering Corp., Somerville, MA, USA) attached to their left wrist with an adjustable sports strap. The participants also wore disposable earplugs (3M 1100), as well as over the head earmuffs (Peltor H7A) for the duration of the experiment in order to prevent them from hearing the operation of the tactor. The tactor was driven by means of a custom-built tactor box connected to the main computer (Dell Technologies). The participants had a Wii Remote (Nintendo Co., Ltd, Kyoto, Japan) attached to their left forearm with another adjustable sports strap. The tactor cable was attached with Velcro to the participant's arm, so that it would not impede the movement of their hand. Both the tactor box and the Wii Remote were interfaced through Matlab (Psychophysics Toolbox 3; Brainard 1997; Pelli 1997) on Windows XP. The Wii communicated with the main computer via bluetooth (BlueSoleil v2), and the communication between the Wii Remote and Matlab was interfaced through the open source library FWIINEUR (fWIIne v0.2; http://fwiineur.blogspot.com/, downloaded on 15 Sept 2009). The auditory signals were delivered via the main computer loudspeaker. The participants gave a vocal response which the experimenter entered into the computer. A set of three juggling balls (5 cm in diameter, 85 g each) was used.

Procedure

The experiment consisted of two sessions: a control (rest) session and an experimental (juggle) session. The participants first performed the control session and, after a short break, continued on to the main experimental session. The rest session lasted for approximately 8–10 min; the participants were seated in a comfortable chair and were offered a cup of tea. In each trial of the rest session, the participants heard an auditory beep (800 Hz, 100 ms) presented from the main computer loudspeaker placed on the floor, to their left. After 1,000 ms, the tactor attached to their wrist vibrated for 2,500 ms. Immediately after the termination of the vibration, a second auditory signal (800 Hz, 100 ms) indicated the end of the trial. The participants had to say whether or not they felt a gap in the vibration. In each trial of the juggling session, the participants had to stand with their forearms held at 90° with respect to their body with their palms oriented toward the ceiling holding the balls (two balls in one hand and the third in the other). An auditory signal (800 Hz, 100 ms) signalled that they should start juggling. The tactor started

vibrating 1,000 ms after the beep. The total duration of the vibration was 3,500 ms. Once the tactor had stopped vibrating, another auditory beep (800 Hz, 100 ms) informed the participants that they should stop juggling. At the end of the trial, the participants again had to give a response with respect to whether or not they felt a gap in the vibration. The experiment continued on to the next trial as soon as the experimenter (seated in a nearby experimental room outside of the participant's sight) had entered their response into the computer.

Design

The rest session consisted of one block of 120 trials. Given the fact that (in the absence of movement) the tactile detection task was very easy, the rest session was conceived of as a familiarization phase, so that the participants could get acquainted with, and hence easily remember, the signal for the following juggle session. In each trial, the TIMING of the gap was manipulated: early (500 ms after the start of the trial), middle (1,000 ms after the start of the trial) or late (1,500 ms after the start of the trial). The second variable that we manipulated was the GAP DURATION: 0 (NO GAP), 10, 20, 30, 40, 60, 70 and 80 ms. The different gap timings, as well as the gap durations, were randomized across trials and participants.

The juggling session consisted of 6 blocks of 32 trials each, adding up to a total of 192 trials. Half of the trials were GAP trials (the vibration was interrupted very briefly), and half of the trials were NO GAP trials (the vibration was continuous). The gap duration was a value drawn randomly from the interval [10:80 ms]. Moreover, half of the GAP trials were 'UP' trials (the gap in the vibration was delivered while the participants' hand was moving upward) and the other half were 'DOWN' trials (the gap in the vibration was delivered while their hand was moving downward). For each of the GAP trials, the TIMING of the gap (1,000, 1,500, 2,000 or 2,500 ms after the start of the vibration) was also manipulated.

Data analysis

For each of the participants, for each of the experimental (rest vs. juggle) sessions, percentages of TP (i.e. YES responses when a gap was present) as well as FP (i.e. YES responses when a gap was not present) were calculated, split considering the manipulated experimental variables (TIMING of the gap for both sessions, together with TYPE of movement for the juggling session). These percentages were then normalized and sensitivity measures (d_a/d'), as well as criterions c, and relative c', were derived according to SDT (Green and Swets 1966; Macmillan and Creelman 2005). See Table 1 for the exact equations used in deriving

Table 1 Equations used to derive the signal detection theory measures in Experiments 1 (E1), 2 (E2) and 3 (E3)

	REST sessions (E1 and E2)	JUGGLE sessions (E1 and E2) and E3
Sensitivity	$d_a = \left(\frac{2}{1+s^2}\right)^{\frac{1}{2}}[z(\text{TP}) - sz(\text{FP})]$	$d' = z(\text{TP}) - z(\text{FP})$
Criterion location	$c = -\frac{1}{1+s}[z(\text{TP}) + z(\text{FP})]$	$c = -\frac{1}{2}[z(\text{TP}) + z(\text{FP})]$
Relative criterion	$c' = \frac{c}{d_a}$	$c' = \frac{c}{d'}$

$z(\text{TP})$ and $z(\text{FP})$ represent the normalized values of the signal present and signal absent trials. The slope (s) is given by the ratio of the standard deviations of signal and noise trials (Green and Swets 1966)

these measures. For the cases when the accuracy was perfect, or no false positives were registered, we adjusted the proportions of 1 and 0 by $1/(2N)$ and $1/(1-2N)$, respectively, where N is the number of trials for a given condition on which the proportion was calculated.

The data were explored, and the assumptions of normality and homogeneity of variance were checked with the Kolmogorov–Smirnov and Levene's tests, respectively. If the normality assumption was violated, non-parametric tests were used to analyse the data. Otherwise, repeated measures analyses of variance (ANOVAs) and t tests were used to examine any differences between the experimental conditions. For these, Mauchly's test of sphericity was used to ensure that the data did not violate the sphericity assumption. If the assumption was violated, then the Greenhouse-Geisser correction was applied to correct the degrees of freedom. Subsequent pairwise comparisons were conducted using the Bonferroni adjustment for multiple comparisons.

The sensitivity and criteria data from the rest session violated the normality assumption. Therefore, Friedman's ANOVA was used on the d' data with the within-participants factors of TIMING of gap (500, 1,000 and 1,500 ms). The same analysis was then conducted on the two criteria data.

The sensitivity data from the juggling session were normally distributed. Therefore, a repeated measures ANOVA was conducted on the d' data with the within-participant factors of TIMING of the gap (1,000, 1,500, 2,000 and 2,500 ms) and TYPE of hand movement (up vs. down). The criteria data calculated for the juggling session violated the assumption of normality. Therefore, related samples Friedman's ANOVAs were conducted on the criterion c and relative criterion c' data.

Finally, Wilcoxon signed ranks tests were conducted on the amalgamated d' data from the two experimental SESSIONS (rest vs. juggling). The same analysis was repeated on the criteria data.

Results

Boxplots of the sensitivity and criteria data from Experiment 1 are presented in Fig. 1.

Rest session: timing of the gap

The analysis revealed that the timing of the gap had no significant effect on the sensitivity data [$\chi^2(2) = 4.2$; $P = .135$]. The same analysis revealed no significant main effect of the timing of the gap on the criterion c data
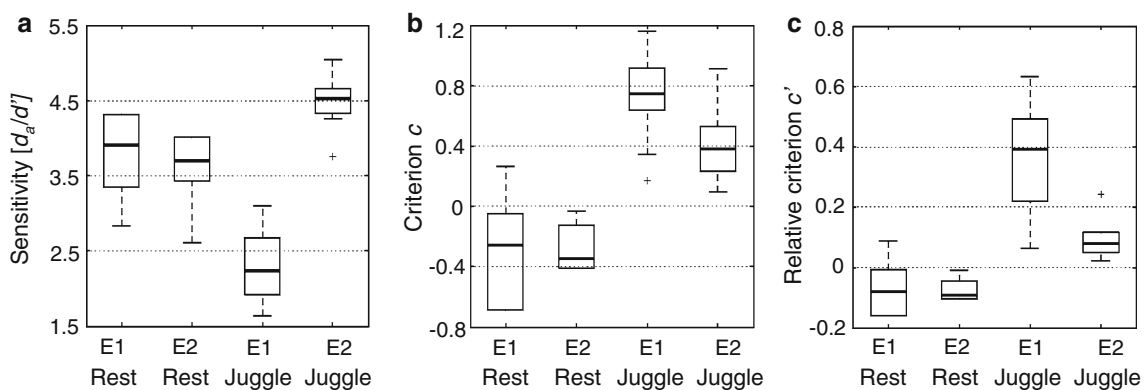

Fig. 1 Boxplots of d' sensitivity data (**a**), criterion c data (**b**) and relative criterion c' (**c**) for Experiments 1 (*E1*) and 2 (*E2*). The *box* represents the middle 50% of the data; the whiskers extend to the *upper* (*top* 25%) and *lower* (*bottom* 25%) quartile, respectively; the *thick horizontal line* denotes the median. Individual data with values higher that 1.5 times the inter-quartiles range are denoted with a '+' sign

$[\chi^2(2) = 5; P = .092]$ and failed to reach significance on the relative criterion c' data $[\chi^2(2) = 3.8; P = .187]$.

Juggle session: timing of the gap

The analysis revealed that the timing of the gap had no significant effect on the sensitivity data $[F(3,27) = .97; P = .423]$. The type of hand movement (up vs. down) was also non-significant in terms of the sensitivity data $[F(1,9) = .17; P = .689]$. Moreover, the interaction between the two experimental variables (the timing of the gap and the type of movement) did not reach significance $[F(3,27) = 1.33; P = .285]$. Furthermore, Friedman's related samples ANOVA revealed no significant difference in upward versus downward movements of the hand for the tested timings of gap delivery on both criterion c data $[F(7) = 9.49; P = .219]$, as well as well as relative criterion c' data $[F(7) = 5.93; P = .548]$.

Rest versus juggle

Participants exhibited significantly higher sensitivity when detecting a gap in the tactile stimulation when this was delivered to the hand at rest ($\mathrm{Mdn_{da}} = 3.90$), as compared to the hand that was juggling ($\mathrm{Mdn_{d'}} = 2.23$; $z = -1.94$, $P = .026$, $r = -.61$). Participants did not, however, shift their criterion in deciding whether there was a gap in the tactile stimulus delivered either when the hands were at rest or while moving, as highlighted by both criterion c data ($z = -1.24$, $P = .117$, $r = -.39$), as well as the relative criterion c' data ($z = -1.48$, $P = .075$, $r = -.46$). Although the criteria effects obtained when comparing the two sessions did not reach statistical significance, note that they both exhibit an above average effect size.

Discussion

With regard to our exploratory aims concerning the dynamics of tactile perception during movement, the results of Experiment 1 revealed no difference in detecting a short gap in an otherwise continuous tactile stimulus between the downward movements ('catches') and upward hand movements ('throws') executed while juggling. At the same time, no difference was found with respect to whether the gap occurred in the beginning, middle or toward the end of the juggling trial. Taken together, the results suggest that when tactile suppression occurs, it is most likely uniformly distributed over the time course of the sustained goal-directed movement, as well as the different types of hand movements used while juggling. However, when comparing the conditions of juggling and rest, the results confirmed our main hypothesis: namely, that tactile perception was impaired when juggling, as

compared to the rest condition (Gallace et al. 2010; Juravle et al. 2010). This clear deterioration observed in tactile perception during movement can be attributed to the motor command and the sensory signals resulting from the performed movement (Chapman and Beauchamp 2006). Alternatively, a more general attentional mechanism could be responsible for the reported effects. Therefore, in order to test for attentional effects, in a second experiment, we used the same experimental paradigm in order to test for a possible 'auditory suppression' phenomenon. The participants in this study had to detect a time gap in a continuous auditory signal, under the same conditions of juggling and rest. If tactile attenuation occurs during movement so that other environmental variables are enhanced, as predicted by the forward models of motor control, then we would expect no deterioration in auditory performance during movement. However, if attention is responsible for the attenuating effects found on tactile perception during movement, then we would expect an equal amount of suppression for the auditory task used in Experiment 2.

Experiment 2

Participants

Nine jugglers (6 male, all right-handed) took part in this experiment (mean age of 27 years; age range 24–34 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. Two of the participants had taken part in Experiment 1. The participants had been juggling for approximately 12 years on average (with a range of 3 months to 20 years). All of the participants were comfortable with basic 3-ball juggling and one participant could competently juggle 4 balls as well.

The *apparatus*, *design* and *procedure* were very similar to those used in Experiment 1 with the following exceptions: (1) The participants wore closed ear headphones (Beyer Dynamic DT 531); (2) The Wii Remote was not used in this experiment, as the first experiment did not show any effect of the type of movement (downward or upward) on sensitivity; and (3) The 2,500 ms vibration delivered in the rest session and the 3,500 ms vibration delivered to the participant's wrist in the juggling session were replaced with auditory signals (800 Hz, 65 dB) of the same duration. The participants now received a short tactile pulse (100 ms) as a signal to start and stop juggling. Their task at the end of the trial was to indicate whether they had heard a gap in the sound or not. All of the other durations and methods were the same as in Experiment 1.

Data analysis

As for Experiment 1, data analysis was conducted on the mean d', as well as criteria c and c'. Since the rest session (as in the case of Experiment 1) violated the normality assumption, Friedman's ANOVA with the within-participants factor of TIMING of the gap (500, 1,000 and 1,500 ms) was conducted on both sensitivity and criteria data. The data from the juggling session were normally distributed. Therefore, repeated measures ANOVAs were conducted on the d' and criteria data with the within-participant factors of TIMING of the gap (1,000, 1,500, 2,000 and 2,500 ms) and TYPE of hand movement (up vs. down). In a next step, Wilcoxon signed ranks tests were conducted on the amalgamated d' and criteria data from the two experimental SESSIONS (rest vs. juggling). A final analysis was conducted in order to compare the results of Experiments 1 and 2. For this analysis, we used independent-samples t tests if the data were normally distributed (sensitivity data in the juggle session of both experiments) or Mann–Whitney tests if they were not (criteria data in the rest and juggle sessions of both experiments).

Results

Boxplots of the sensitivity and criteria data from Experiment 2 are presented in Fig. 1.

Rest session: timing of the gap

The analysis revealed that the timing of the gap delivery had no significant effect on the d' sensitivity measure [$\chi^2(2) = 2.66$; $P = .44$]. Moreover, this analysis did not reach significance for either criterion c data [$\chi^2(2) = 0$; $P = $ n.s.] or criterion c' data [$\chi^2(2) = 0$; $P = $ n.s.].

Juggle session: timing of the gap

The analysis showed that the timing of the gap had no significant effect on either the d' data [$F(3,24) = 0$; $P = $ n.s.], criterion c [$F(3,24) = 0$; $P = $ n.s.] or criterion c' [$F(3,24) = 0$; $P = $ n.s.].

Rest versus juggling

The analysis revealed a significant effect of the experimental session on d' data [$z = -2.31$, $P = .021$, $r = -.77$], with participants exhibiting significantly higher sensitivity for a gap in auditory stimulation delivered in the juggle condition (Mdn$_{d'}$ = 4.52), as compared to the rest condition (Mdn$_{da}$ = 3.70). The same effect did not reach significance for the criterion c data [$z = -1.40$, $P = .161$,

$r = -.46$] and showed a marginally significance on criterion c' data [$z = -1.89$, $P = .058$, $r = -.63$].

Comparison of the results of Experiments 1 versus 2

Rest session

Participants showed no significant difference in their sensitivity between detecting a gap in tactile stimulation and detecting a gap in auditory stimulation at rest [Mdn$_{da}$ = 3.84, $U = 36$, $P = .241$, $r = -.17$]. Moreover, no significant difference was found between the criterion c adopted in the rest sessions of Experiments 1 and 2 [Mdn$_c$ = .34, $U = 43$, $P = .443$, $r = -.03$], nor was there any effect for the relative criterion c' [Mdn$_{c'}$ = -.09, $U = 42$, $P = .412$, $r = -.05$].

Juggling session

The analysis revealed a significant difference in the d' means from the juggling sessions of the two reported experiments [$t(17) = -10.52$, $P < .001$, $r = .93$], with participants being less sensitive to detect a gap in the vibration delivered to their wrist, as compared to a gap in the auditory signal. Moreover, a significant difference was found for the criterion c data [Mdn$_c$ = 0.53, $U = 17$, $P = .010$, $r = -.52$] from the juggling sessions of the two experiments, with participants being significantly less conservative in saying that there was a gap in the stimulation in Experiment 2 as compared to Experiment 1. Finally, criterion c' data showed a similar significant pattern [Mdn$_{c'}$ = 0.20, $U = 7$, $P < .001$, $r = -.71$]: If participants' criterion c' was more or less clustered around the zero-bias point for the auditory gap detection while juggling, their criterion was significantly shifted toward saying NO in the tactile gap detection task, performed in Experiment 1.

Discussion

The results of Experiment 2 indicate that participants are significantly more sensitive while juggling to detect a gap in auditory stimulation, as compared to the rest condition. Such a result could be taken to support the forward models of motor control hypothesis (Miall and Wolpert 1996; Wolpert et al. 1995). According to such models, movement of our limbs brings suppression for the information related to the movement itself (e.g. tactile information), but at the same time, it has been suggested that movement favours enhancement of external stimuli (e.g. auditory information). However, the interpretation of the results of the rest versus juggle sessions of Experiment 2 needs to be taken with some caution. Note that the sensitivity data of the rest

sessions (in both Experiments 1 and 2) are derived from unequal number of true and false positives, a fact that most probably led to an underestimation of the real sensitivity performance for the two rest sessions and consequently the significant difference between the two sessions in Experiment 2. Nevertheless, when comparing the normally distributed data form only the juggle sessions of Experiments 1 and 2, a significant deterioration in participants' performance was found for Experiment 1. Such results could, therefore, be interpreted as a consequence of the motor command. Also, more importantly, the results highlighted the fact that participants clearly shifted their criterion toward saying that no gap was present in tactile stimulation while juggling in Experiment 1, as compared to the auditory stimulation in Experiment 2.

In order to control for the limitations inherent in the rest conditions (of both Experiments 1 and 2), in Experiment 3, participants performed the same gap detection task, this time by always keeping their hands at rest. Perceptual sensitivity, together with response bias, was tested with an equally balanced task comprising auditory and tactile conditions. We hypothesized that participants would exhibit comparable sensitivity for the auditory and tactile gap detection tasks. However, at the same time, another factor that could account for the suppression found in our data could be intramodal tactile suppression, e.g., the sensory feedback received when the ball touched the hand while juggling cannot be fully accounted for by the rest condition of Experiment 1. Therefore, in order to control for this alternative explanation, in an additional condition in Experiment 3, participants performed the tactile gap detection task, while the experimenter rhythmically touched their palms with two juggling balls.

Additionally, we were also interested in investigating whether the duration of the gap (a variable that was randomly allocated in both Experiments 1 and 2) influences the measured sensitivity, as well as criterion allocation.

Experiment 3

Participants

Ten participants (3 male, one left handed) took part in this experiment (mean age of 27 years; age range 23–28 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. None of the participants was familiar with juggling at the time of participation. The experiment lasted approximately 40 min, and participants received a £5 gift voucher in return for taking part in the study.

The *apparatus* was the same as for Experiments 1 and 2. The *design* and *procedure* (including the timeline of the

trial) were very similar to those used in the juggle sessions of the first two experiments. Therefore, in the following, we will only highlight the methodological differences between the studies. Experiment 3 consisted of three separate conditions, all involving the detection of a temporal gap in auditory stimulation (Experiment 3a), tactile stimulation (Experiment 3b) or tactile stimulation plus tactile interference (Experiment 3c). The order in which the conditions were presented was counterbalanced across participants. All three conditions involved no movement of the hands; the participants were seated at a table with both hands on the table surface, their palms facing upward.

In each trial of Experiment 3c, the experimenter, seated across the table in front of the participant, touched the participant's palms with two juggling balls. For this, the experimenter held a stick with one ball attached at either end. For the duration of the trial, the experimenter balanced the stick so that the balls touched the palms of the participant's hand in a rhythmical fashion; the balancing movement of the stick was kept as constant as possible, and the resulting touches were intended to mimic the touch of the balls from the juggle session, in the absence of any overt movement by the participant. The vibratory tactile stimulation, as well as the auditory stimulation, was the same as in the first two experiments. Each of the three conditions consisted of two blocks of 60 trials each. Half of the trials in each block were target absent trials (i.e. no gap in stimulation was delivered), while the other half of the trials were target present trials (i.e. there was a short time gap in the tactile or auditory stimulation). The only manipulated variable was the duration of the gap (20, 40, or 60 ms). Given the fact that the first two experiments showed no significant difference in sensitivity, nor in response bias for the different timings of the gap delivery within the trial, in Experiment 3, the timing of the gap was allocated randomly.

Data analysis

The data analysis was conducted on the mean d', as well as criteria c and c' data. If the data did not violate the normality assumption, in a first step, the data from each condition were analysed with repeated measures ANOVAs with the factor GAP DURATION (20, 40, or 60 ms). When the normality assumption was violated, the non-parametric Friedman's ANOVA was used instead. A second analysis was conducted on the amalgamated data from the three conditions, with the factor CONDITION (auditory, tactile and tactile-ball interference). For this, we used Friedman's ANOVA and we followed up with Wilcoxon signed ranks tests to investigate differences between the three conditions.

Results

Boxplots of the sensitivity and criteria data from Experiment 3 are presented in Fig. 2.

Experiment 3a: gap duration

For the auditory condition, the Kolgomorov–Smirnov test indicated the violation of the normality assumption for all the measures of performance used. Participants showed no significant difference in their sensitivity in detecting the three different duration gaps $[\chi^2(2) = 1.62; P = .580]$. Moreover, no significant difference was found for participants' criterion c $[\chi^2(2) = 1.62; P = .580]$ or criterion c' $[\chi^2(2) = 2.37; P = .457]$.

Experiment 3b: gap duration

For the tactile condition, participants showed no significant difference in their sensitivity in detecting the three different duration gaps $[F(2,18) = 1; P = .387]$. The same non-significant difference was found for participants' criterion c $[\chi^2(2) = 2; P = .556]$ and criterion c' $[\chi^2(2) = 0; P = \text{n.s.}]$.

Experiment 3c: gap duration

For the tactile-ball interference condition, participants showed no significant difference in their sensitivity in detecting the three different duration gaps $[F(2,18) = .04; P = .959]$. The same non-significant difference was found for participants' criterion c $[F(2,18) = .04; P = .959]$, as well as criterion c' $[F(2,18) = .07; P = .936]$.

Comparison of the results of Experiments 3a versus 3b versus 3c

The analysis of the sensitivity data from the three conditions of Experiment 3 revealed a significant main effect of

condition $[\chi^2(2) = 12.47; P = .001]$. Post hoc tests showed that participants' sensitivity in the tactile-ball interference condition ($\text{Mdn}_{d'} = 3.71$) was significantly lower as compared to the auditory condition $[\text{Mdn}_{d'} = 4.68, z = -2.86, P = .001, r = -.90]$ and the tactile condition $[\text{Mdn}_{d'} = 4.47, z = -2.36, P = .012, r = -.74]$. No significant difference was documented between the sensitivity in detecting a gap in auditory versus tactile stimulation $[z = -1.15, P = .199, r = -.36]$. The criterion data revealed no difference between the three tested conditions on both criterion c $[\chi^2(2) = .36; P = .897]$ and criterion c' $[\chi^2(2) = .46; P = .806]$.

Discussion

The results of Experiment 3 highlight comparable sensitivity when participants tried to detect a short temporal gap presented in tactile and auditory stimulation at rest. This result is important because it shows that for the task employed in the present study, performance at rest when equal numbers of target absent and target present trials are used (Experiments 3a and 3b), does clearly take a ceiling pattern. With regard to our familiarization rest sessions from Experiments 1 and 2, it has been shown that the different presentation probabilities can affect both sensitivity, as well as response bias (see Macmillan and Creelman 2005, for a discussion). Moreover, the sensitivity values recorded in these two control conditions of Experiment 3 are comparable to the sensitivity values from the juggle session of Experiment 2, suggesting that the hand movements in the case of the auditory temporal gap detection task are not a factor affecting sensitivity. At the same time, the sensitivity data in our tactile-ball interference condition were significantly lower as compared to the other two conditions. This result supports the claim regarding the tactile intramodal hypothesis, according to which not only the movement but also the balls touching
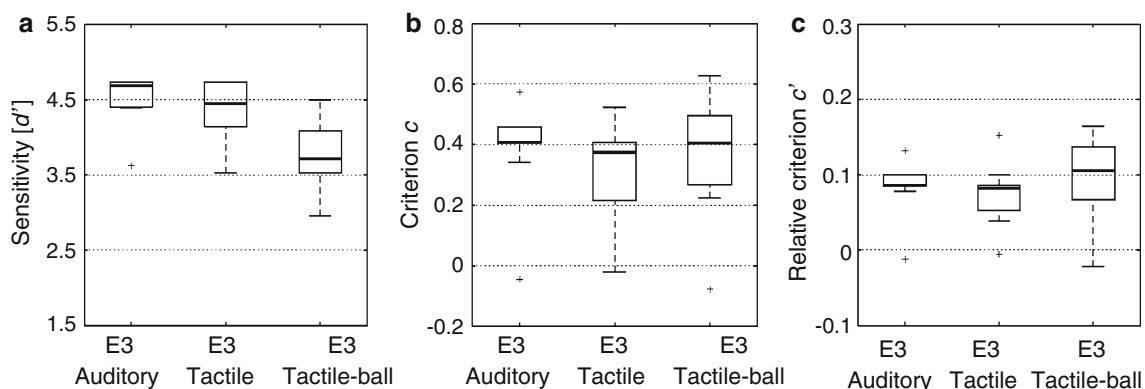

Fig. 2 Boxplots of d' sensitivity data (**a**), criterion c data (**b**) and relative criterion c' (**c**) for Experiment 3 (*E3*). The *box* represents the middle 50% of the data; the whiskers extend to the *upper* (*top* 25%) and *lower* (*bottom* 25%) quartile, respectively; the *thick horizontal line* denotes the median. Individual data with values higher that 1.5 times the inter-quartiles range are denoted with a '+' sign

the hands, contributed to the deterioration in tactile sensitivity experienced while moving. However, more importantly, the criteria results of Experiment 3 revealed no difference in participants' criteria allocation between the three conditions: Though slightly above zero, and thus indicating a tendency to respond 'NO', participants' criterion could be considered more or less unbiased.

General discussion

The present study investigated tactile suppression by using a complex bimanual juggling task. The first conclusion that can be drawn from the results reported here is that tactile suppression is a robust empirical phenomenon that appears during the execution of complex motor skills, such as basic 3-ball juggling. This outcome was to be expected. It has previously been shown that tactile perception deteriorates during the execution of simple finger movements (Voss et al. 2006), as well as during more complex goal-directed movements (Gallace et al. 2010; Juravle et al. 2010). Recently, a study that investigated the detection of threshold vibratory stimuli during the execution of bimanual visual pointing movements showed a similar pattern of results, with the greatest suppression effects clustered around the onset of the movement (Buckingham et al. 2010). When considering the juggle session of both Experiments 1 and 2 of the present study, performance clearly deteriorated for the tactile task, as compared to the almost perfect performance observed in the auditory task. These results favour the forward models of motor control account, indicating that the experienced deterioration in what is felt while juggling most probably results from a combination of the motor command and the sensory signals resulting from the self-generated movements themselves (Chapman and Beauchamp 2006).

The sensitivity measured at rest in the tactile-ball interference condition nevertheless indicates that a tactile intramodal mechanism acts on tactile perception and significantly disrupts performance, in the absence of movement. Indeed, in this respect, neuroimaging studies investigating tactile perception indicate that this tactile intramodal interference is most likely the consequence of inhibitory connections between the two somatosensory cortices (see Hlushchuk and Hari 2006; Kastrup et al. 2008; Klingner et al. 2010, 2011). Nevertheless, the magnitude of the deterioration in sensitivity for the juggle session of Experiment 1 is clearly higher than that observed in Experiment 3c. This result suggests that although tactile intramodal interference contributes to the tactile suppression effects observed while juggling, it does not fully account for it. Moreover, if one considers the criteria data

from all the conditions of our control study (Experiment 3), one can easily notice that while at rest, participants are no more inclined to say that the gap was absent when passively touched with the juggling balls (and thus having the tactile intramodal interference at play), as compared to the simple tactile gap detection.

On the other hand, participants' criterion was significantly shifted from the point of zero-bias in the juggle session of Experiment 1. This result is important because it indicates that movement itself is the delineating factor in defining tactile suppression and consequently the criterion shift. Therefore, if participants were less sensitive in detecting a gap in the tactile stimulus while they were moving their limbs, they were, at the same time, less inclined, or more conservative, in reporting it. This decisional component of the suppression effect provides evidence against a purely physiological account of suppression and could again be taken to argue in favour of a decision-based modulation of the phenomenon. At a neural level, it is known that sensory evidence concerning tactile stimulation accumulates in the somatosensory cortex (S1), while the primary motor cortex (M1) is involved in the preparation and execution of behavioural motor responses. Efferent signals for sensory suppression have been localized to the primary motor cortex (Voss et al. 2007), as well as the medial supplementary motor area (Haggard and Whitford 2004), thus linking sensory suppression to the stage of motor planning and execution. Moreover, it has been shown that other adjacent brain areas that connect sensory input to motor output are also involved in the process of decision making. For example, Romo and Salinas (2001) have demonstrated that the activity recorded in primates' motor areas correlates with their performance in decision-making tasks, suggesting that decisions may occur at a sensory-motor interface. Furthermore, decisional processes have been tracked down to the ventral and medial prefrontal cortex, since activity in these regions has been shown to be influenced not only by the quality of tactile stimulation but also, and most importantly, the activity correlated with the monkey's behavioural response: for example, cells in the medial premotor cortex, a region also known as the supplementary motor area, had enhanced firing patterns for tactile stimulation that was acknowledged by the monkey as a 'stimulus present trial', or a true positive response (de Lafuente and Romo 2005; Romo et al. 2004). It appears that at a physiological level, the same brain areas usually involved in motor control are also involved in a decision-making process.

Lastly, the results outlined here, demonstrating suppression during juggling, allow us to postulate an interesting hypothesis. As highlighted in the present study,

tactile perception deteriorates during complex goal-directed movements, such as basic 3-ball juggling. This phenomenon is independent of any contribution from overt visual attention, since direct visual input from the hand is not available while juggling. Some peripheral vision of the moving hands is of course still used while juggling, given that the eyes are needed to monitor the peaks of the juggling balls. Therefore, it seems that one has to consider the contribution of the other senses to the on-going sustained movement. In this respect, it could be that proprioception is the main 'pillar' of the rhythmical movement involved in three-ball juggling. Indeed, it has been shown that when moving in depth, people find it easier to localize the hand when it is positioned closer to the shoulder, as compared to more distant locations (Van Beers et al. 1998). Moreover, older studies examining the acquisition of a new motor skill (e.g. fencing) have shown significantly improved performance under conditions of proprioception alone (i.e. under conditions of blindfolding), as compared to conditions of vision alone, or vision and proprioception combined (Jordan 1972). From this view point, juggling could be considered as a promising area to research how the senses come together/apart while moving. A possible demarcation between the traditional *spatial* multisensory integration at rest as opposed to a *movement-related* sensory interference could be further drawn: If information from the different sensory modalities is integrated according to the well-known spatial, temporal and inverse effectiveness rules (see Holmes and Spence 2005; Stein and Meredith 1993), it would appear that while moving we could at most speak of multisensory interference or intersensory dominance.

To conclude, the present study provides evidence of tactile suppression occurring during the rhythmical execution of bimanual movements, characteristic of 3-ball juggling. The reported attenuating effect on tactile perception is most likely a combination of the juggle movement itself (Experiment 1) and the sensory feedback of the juggling balls touching the hands while juggling (Experiment 3c). The deterioration in tactile sensitivity for the juggling session of the present study was accompanied by a significant conservative shift in participants' criterion (i.e. more likely to give a 'NO' response). This result indicates a decisional component to tactile suppression, suggesting that suppression could already be triggered in the brain ahead of the motor command. Looking for tactile suppression in frontal areas would, therefore, provide a means of investigating the neuronal correlates of this phenomenon using a more brain-related method.

References

Bays PM, Wolpert DM (2007) Computational principles of sensoriomotor control that minimize uncertainty and variability. J Physiol 578:387–396

Brainard DH (1997) The psychophysics toolbox. Spatial Vis 10:433–436

Brozzoli C, Pavani F, Urquizar C, Cardinali L, Farnè A (2009) Grasping actions remap peripersonal space. Neuroreport 20:913–917

Buckingham G, Carey P, Colino FL, deGrosbois J, Binsted G (2010) Gating of vibrotactile detection during visually guided bimanual reaches. Exp Brain Res 201:411–419

Chapman CE, Beauchamp E (2006) Differential controls over tactile detection in humans by motor commands and peripheral reafference. J Neurophysiol 96:1664–1675

de Lafuente V, Romo R (2005) Neuronal correlates of subjective sensory experience. Nat Neurosci 8:1698–1703

Gallace A, Zeeden S, Röder B, Spence C (2010) Lost in the move? Secondary task performance impairs tactile change detection on the body. Conscious Cogn 19:215–229

Green DM, Swets JA (1966) Signal-detection theory and psychophysics. Wiley, New York

Haggard P, Whitford B (2004) Supplementary motor area provides an efferent signal to sensory suppression. Cogn Brain Res 19:52–58

Hlushchuk Y, Hari R (2006) Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation. J Neurosci 26:5819–5824

Holmes NP, Spence C (2005) Multisensory integration: space, time and superadditivity. Curr Biol 15:R762–R764

Jordan TC (1972) Characteristics of visual and proprioceptive response times in the learning of a motor skill. Q J Exp Psychol 24:536–543

Juravle G, Deubel H, Tan HZ, Spence C (2010) Changes in tactile sensitivity over the time-course of a goal-directed movement. Behav Brain Res 208:391–401

Kastrup A, Baudewig J, Schnaudigel S, Huonker R, Becker L, Sohns JM, Dechent P, Klingner C, Witte OW (2008) Behavioral correlates of negative BOLD signal changes in the primary somatosensory cortex. Neuroimage 41:1364–1371

Klingner CM, Ebenau K, Hasler C, Brodoehl S, Görlich Y, Witte OW (2011) Influences of negative BOLD responses on positive BOLD responses. Neuroimage 55:1709–1715

Klingner CM, Hasler C, Brodoehl S, Witte OW (2010) Dependence of the negative BOLD response on somatosensory stimulus intensity. Neuroimage 53:189–195

Macmillan NA, Creelman CD (2005) Detection theory: a user's guide, 2nd edn. Lawrence Erlbaum Associates, Mahwah

Miall RC, Wolpert DM (1996) Forward models for physiological motor control. Neural Netw 9:1265–1279

Pelli DG (1997) The video toolbox software for visual psychophysics: transforming numbers into movies. Spatial Vis 10:437–442

Romo R, Hernandez A, Zainos A (2004) Neuronal correlates of perceptual decision in ventral premotor cortex. Neuron 41:165–173

Romo R, Salinas E (2001) Touch and go: decision-making mechanisms in somatosensation. Annu Rev Neurosci 24:107–137

Stein BE, Meredith MA (1993) The merging of the senses. MIT Press, Cambridge

Van Beers RJ, Sitting AC, Denier van der Gon JJ (1998) The precision of proprioceptive position sense. Exp Brain Res 122:367–377

Voss M, Bays PM, Rothwell JC, Wolpert DM (2007) An improvement in perception of self-generated tactile stimuli following theta-burst stimulation of primary motor cortex. Neuropsychologia 45:2712–2717

Voss M, Ingram JN, Haggard P, Wolpert DM (2006) Sensorimotor attenuation by central motor command signals in the absence of movement. Nat Neurosci 9:26–27

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensoriomotor integration. Science 269:1880–1882