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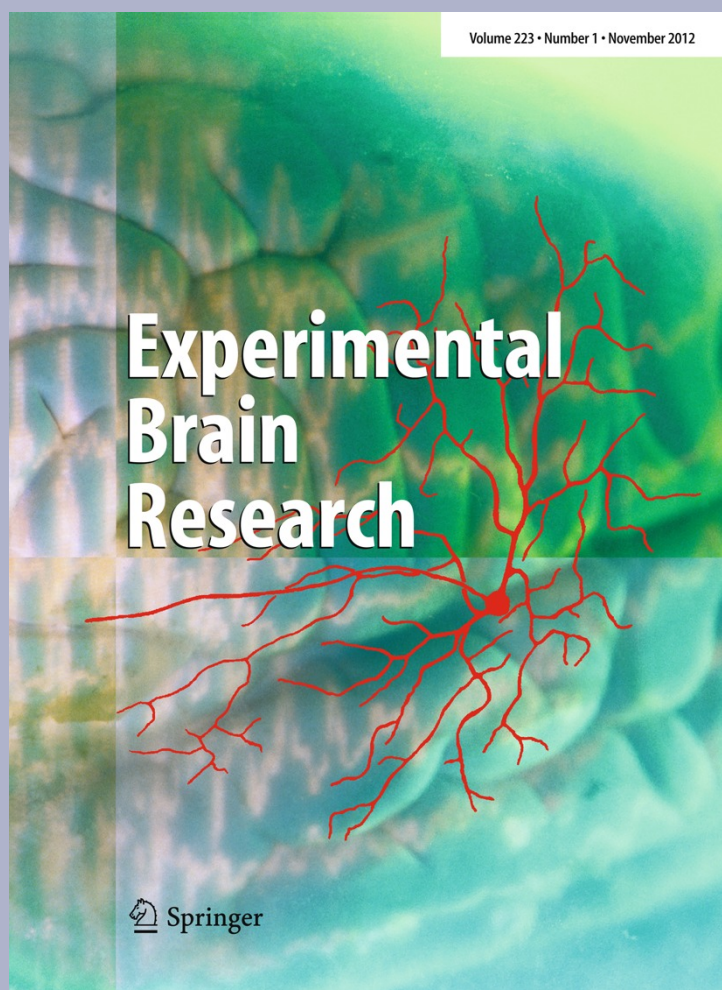
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Perceptual and decisional attenuation of tactile perception during the preparation of self- versus externally-generated movements

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Abstract We investigated tactile perception during the execution of self- versus externally-generated movements. In a first experiment, we established the temporal characteristics of the movements of interest. In a second experiment, participants had to try to detect a short gap in an otherwise continuous vibratory stimulus delivered to their right wrist under conditions of rest, throwing (i.e., self-initiated movement), or catching a basketball (i.e., externally-generated movement). Our hypothesis was that different patterns of tactile sensitivity (d') and response bias (criteria c and c') would be observed as a function of the timing of gap delivery (i.e., during movement preparation or movement execution) and the type of movement (self- or externally-generated). A third experiment investigated tactile perception at rest while participants adopted different hand postures. This experiment also tested the simple preparation of the self-/externally-generated movements versus the observation of these targeted movements as performed by the experimenter. Due to sensory suppression, participants were significantly less sensitive in detecting the gap in tactile stimulation while executing the movement. Preparing to catch the ball only triggered a shift in response bias (i.e., participants were more liberal/conservative when reporting the gap in stimulation), but no change in perceptual sensitivity was observed, as compared to rest. Preparing to make a ball-throwing movement resulted in a significant decrement in tactile sensitivity, as well as a shift in participants' criterion toward their being more conservative, when responding to the presence of the target. Similar decrements were

observed for the observation of self-initiated movement preparation, but not for the observation of their externally-generated counterparts. Taken together, these results demonstrate that different forms of attenuation influence tactile perception, depending on the type of movement that is executed: *perceptual* and *decisional* attenuation for self-initiated movements, but only *decisional* attenuation for externally-generated movements. These results suggest that the movement preparation sensorimotor contingencies are already modulated in prefrontal decision-related cortical brain areas.

Keywords Sensory suppression · Tactile · Response bias · Externally-generated movement

Introduction

Goal-directed movements are characterized by decreased tactile sensitivity in humans (Buckingham et al. 2010; Gallace et al. 2010; Juravle et al. 2010, 2011). This phenomenon, known as tactile suppression/attenuation (or tactile gating), is thought to result from a combination of movement-related gating (i.e., attributable to the efference copy), and peripheral gating (i.e., associated with the sensory signals arising from the self-generated movements; see Chapman and Beauchamp 2006 for a discussion).

Tactile suppression has been shown to follow a different temporal pattern during the different phases of a goal-directed movement (Juravle et al. 2010). Recently, Juravle et al. (2011) examined the preparation period of a goal-directed reach-to-grasp movement, investigating whether the mere preparation to move resulted in any change in tactile perceptual sensitivity in the movement effector. Their results highlighted a similar decline in tactile

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sensitivity in the movement preparation period for those conditions in which the participants had prepared the movement, but had not yet selected the movement effector, and those conditions in which participants had prepared the movement and the selection of the movement effector had already taken place. Such results demonstrate that tactile suppression is already present at the movement effector in the preparation period of a goal-directed reach-to-grasp movement. The movements used in this and other studies that have reported tactile gating during the execution of goal-directed movements have always been self-initiated.

Nevertheless, at a behavioral level, self-initiated actions can clearly be dissociated from externally-generated actions. At a neural level, increased activation is seen in several brain regions during the execution of the two types of movement. For the internally generated actions, these include an extensive network of brain areas such as the left primary sensorimotor cortex, supplementary motor area, the anterior cingulate, the lateral premotor cortex, the left thalamus and putamen, parietal area 40, and the right dorsolateral prefrontal cortex (Jahanshahi et al. 1995). The same areas are also seen to be active during the execution of externally triggered movements. The only difference being that a superior activation is observed in the dorsolateral prefrontal cortex in self-initiated, as opposed to the externally-generated, movements (Jahanshahi et al. 1995; see also Deiber et al. 1999; Jenkins et al. 2000, for a discussion of the role that dorsal frontal regions play in motor preparation and motor execution). A stronger EMG signal has also been reported for self-initiated movements, leading Obhi and Haggard (2004) to suggest that these actions might simply be more forceful than their externally-generated counterparts.

Specifically with regard to the topic of tactile perception, to our knowledge, no other study has contrasted self-initiated versus externally triggered movements, in order to highlight the respective characteristics of tactile perception in the two cases. Note that the gating of other somatic inputs, such as thermal stimulation (i.e., judgments of 'coldness,' VanDoorn et al. 2005), as well as painful stimulation (Helmchen et al. 2006), has been reported during the execution of self-initiated movements.

In the present study, we used signal detection theory (SDT, Green and Swets 1966) in order to examine the characteristics of tactile perception as they unfold during the execution of self-initiated versus externally triggered hand movements. When analyzing two discrete states of the world (e.g., either a *signal* is present, such as the gap in the vibratory stimulation used in this study, or a signal is absent, or *noise* is present), states that cannot be easily distinguished, SDT provides an ideal means of delineating between the two. The combination of these two discrete

states and the two categories of response with regard to the presence of the stimulus (YES and NO) generates four classes of combined events: true positives, false positives, false negatives, and true negatives. The psychophysical model of SDT therefore points toward there being two stages of information processing involved in target detection (Green and Swets 1966): First, we gather *sensory evidence* concerning the presence or absence of a signal and second, we make a *decision* about whether or not the signal is present.

As such, SDT allows researchers to derive measures not only of sensitivity (d') but also of response bias (criteria c or c' , see Macmillan and Creelman 2005) in the tested domain, under various experimental conditions. Consequently, SDT offers a valuable method with which to discriminate between participants' true sensitivity to physical stimulation (i.e., the stimulus-based *perceptual* component) and their bias toward responding in a certain way when deciding on the type of stimulation (i.e., the participant-dependent *decisional* component). Having a signal detection paradigm is crucial if one is interested in investigating the nature of tactile attenuation that is found to affect the preparation and execution of goal-directed movements (Juravle et al. 2010, 2011; Juravle and Spence 2011). Note that earlier studies on tactile attenuation have investigated tactile sensitivity without taking into account participants' criterion, or their inclination toward reporting the presence of a tactile stimulus or of a change in the on-going tactile stimulation, in the absence of it (e.g., Williams and Chapman 2000, 2002). As such, participants can adopt a liberal criterion when performing the task (i.e., they will be inclined to respond YES) or a conservative criterion (i.e., they will be inclined to respond NO). This is reflected in the criteria distribution: Negative values of criteria c/c' indicate the tendency to say YES, whereas positive values indicate the tendency to give a negative response; criteria values of 0 indicate a lack of criterion shift for the tested experimental variables. When sensitivity differs between experimental conditions, the appropriate measure of response bias is the relative criterion c' (i.e., criterion c scaled by the corresponding sensitivity; Macmillan and Creelman 2005).

Having established differential components of tactile attenuation during movement execution (Juravle and Spence 2011), in the present study we set out to determine whether similar decisional/perceptual decrements would affect the preparatory phase of a goal-directed movement. Furthermore, given the extensive neuroimaging evidence of differential brain structures contributing to the planning and execution of self- versus externally-generated movements (Deiber et al. 1999; Jahanshahi et al. 1995; Jenkins et al. 2000), we were interested in investigating whether tactile perception is differentially modulated by the

preparation to perform either self- or externally-generated movements. We hypothesized that if the decrement in tactile perception occurring before movement initiation is due only to the generation of the motor command (Chapman and Beauchamp 2006), then a perceptual decrement would be observed during the preparatory phase of the movement. However, if the deterioration in what is felt results from an internal criterion shift related to the participant's expectation with regard to the outcome of the movement, then a decisional decrement in tactile perception ought to be observed during the preparatory phase of the movement.

Therefore, in a first control experiment, we defined the temporal windows of self- (i.e., ball-throwing) and externally-generated movements (i.e., ball-catching) to be used for the following experiments involving tactile stimulation. For this, the participants had to perform ball-throws/catches following a sequence of prepare/go auditory signals, and their movement coordinates were recorded. These movements were specifically chosen for their key characteristics: Throwing constitutes a natural self-initiated movement, and at the same time, the catch occurs as a natural reactive movement to the approach of the ball. The movements utilized in the present study can therefore be said to be ecologically valid.

Experiment 1

Methods

Participants

Ten participants (4 male, all right-handed) took part in this experiment (mean age of 23 years; age range: 18–28 years). All of the participants reported normal touch, normal hearing, as well as normal or corrected to normal vision. None of the participants was a member of an athletics club. The experimental session lasted for approximately 20 min and the participants received £3 (British pounds) or course credit in return for taking part in the study.

Apparatus

The experiment took place in a wide, well-lit room. The participant and the experimenter (the same for all participants) were standing, facing each other, with a distance of approximately 2.7 meters separating them. Both the participant and the experimenter wore closed ear headphones (Beyer Dynamic DT 531) for the duration of each block of trials during the course of the experiment. The participants had a Wii Remote with an additional Wii Motion Plus (Nintendo Co., Ltd, Kyoto, Japan) attached to their right forearm by means of an adjustable sports strap. The Wii

accelerometer (± 3 g sensitivity range, 8 bits per axis, 100 Hz update rate, Lee 2008) and the additional Motion Plus sensor were interfaced through Matlab (Psychophysics Toolbox 3; Brainard 1997; Pelli 1997) on Windows XP. The Wii communicated with the main computer via Bluetooth (IVT BlueSoleil v2), and the communication between the Wii Remote-Wii Motion Plus and Matlab was interfaced through the open source library FWIINEUR (fWIIIne v0.4; <http://fwiineur.blogspot.com/>, downloaded in July 2010). A men's basketball (Adidas; approximately 75 cm in diameter) was used.

Procedure and design

The experiment consisted of two conditions: A *catch* condition and a *throw* condition, with the order of presentation of the conditions counterbalanced across participants. Each of the conditions consisted of one block of 30 trials amounting to a total of 60 trials per experiment. The participants were allowed a short break in between the blocks.

In the catch condition, participants were instructed to start each trial with their arms at their sides. In the throw condition, participants started each trial with both hands holding the ball to their chest. Conversely, in the catch condition, the experimenter started the trial with both hands holding the ball. Participants were instructed to perform the movement as smoothly as possible, that is, to slowly bring their hands to their sides after the throw of the ball, or to keep the ball in their hands after they caught it, until the signal marking the end of the trial.

Each trial started with an auditory signal (*start signal*; 50 ms, 400 Hz). This was followed after a 2,290 ms stimulus onset asynchrony (SOA) by a second higher-pitched auditory signal (*go signal*; 50 ms, 800 Hz). In the *catch condition*, the go signal was for the experimenter's benefit. The experimenter threw the ball at the participant (i.e., a standard chest pass in basketball, aimed at the participant's chest) and the participant was instructed to catch it when it arrived in his/her vicinity. In the *throw condition*, the go signal was for the benefit of the participant. The participant threw the ball at the experimenter, who caught it when it approached. Note that the go signal always instructed either the experimenter or participant to *throw* the ball. A *final* auditory signal (50 ms, 800 Hz) was delivered 2,100 ms after the go signal, in order to mark the end of the trial.

At the end of the trial, depending on the condition, the participant returned the ball to the experimenter (in the catch trials) or the experimenter returned the ball to the participant (in the throw trials). The experiment went on to the next trial once the experimenter pressed a key on the keyboard.

Data analysis and results

Given the nature of the goal-directed movements performed—both involving rotational wrist/arm movements, we were interested in analyzing the motion 3D data acquired by the Wii Motion Plus (i.e., the *x*-axis *roll* orientation movement). For each participant, for every trial, the roll data were referenced in time to the delivery of the go signal to throw the ball—the value recorded at time 0 was thus taken as the baseline for movement initiation calculations. We then extracted the point in time at which the roll rotation movement exceeded 50 degrees from the baseline and defined this as the reaction time (RT) to initiate the movement. That is, for both types of movements tested here (ball-catching versus ball-throwing), the RT to initiate the required movement was calculated from the go signal to throw the ball. We then averaged the RTs for each condition and each participant. In a last step, we calculated the mean RTs across participants. Figure 1 shows a depiction of the averaged movement trajectories for the two ball-catching and ball-throwing movements.

Participants initiated the ball-throwing movement on average 539 ms (SE = 43 ms) after the delivery of the go signal, and they initiated the ball-catching movement 1,030 ms (SE = 48 ms) after the signal to move. In Experiment 2, we used these times to initiate the movement for the separation between the preparatory and execution phases of the two movements of interest.

As such, in Experiment 2, tactile perception was addressed in the context of a similar paradigm to that used in Experiment 1 involving participants catching or throwing a ball. In an additional control condition, the movement of the participants' hands was restrained and the perceptual task was performed at rest, while the participants stood with their arms at their sides. Tactile sensitivity, together with response

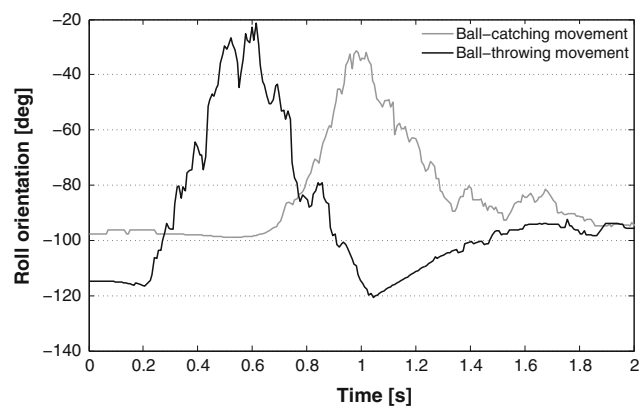


Fig. 1 Mean accelerometer roll orientation movement data for the two movements (ball-catching versus ball-throwing) tested in Experiment 1, plotted against time. Time 0 represents the delivery of the go signal to throw the ball

bias, was assessed at different points in time for the two movements: in the preparation period (i.e., when movement per se was not yet initiated) and in the movement execution period. We hypothesized that a decrement in tactile sensitivity would be observed during the movement execution period, together with a change in response bias (Juravle and Spence 2011). Moreover, for the preparation period, we were interested in investigating whether a differential pattern of results from the SDT analysis would be observed when the movement resulted from the participant's own volition, as compared to when it was externally-generated. By comparing the preparatory phases of throwing and catching movements, we hoped to disentangle the potential perceptual and decisional components of tactile suppression.

Experiment 2

Methods

The methods of Experiment 2 are very similar to those used in Experiment 1. Therefore, only the differences are described here.

Participants

Fourteen participants (5 male, one left-handed) took part in this experiment (mean age of 26 years; age range 23–32 years). The experimental session lasted for approximately 40 min, and the participants received a £5 (British pounds) gift voucher in return for taking part in the study.

Apparatus

The participants had one tactor (VBW32 skin stimulator, 1.6 × 2.4 cm vibrating surface, Audiological Engineering Corp., Somerville, MA, USA) attached with an adjustable sports strap to the ventral part of their right wrist. The participant's wrist was then covered with several layers of thin sponge in order to reduce the possibility that they would be able to hear 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 tactor cable was attached with Velcro to the participant's arm so that it would not impede their hand movements. Two loudspeakers were positioned on a table on either side of experimenter's back. The participants gave a vocal response, which the experimenter entered into the computer.

Procedure

The experiment consisted of three conditions: a control (*rest*) condition and two experimental conditions (a *catch*

condition and a *throw* condition), with the order of presentation of the conditions counterbalanced across participants. The vibratory signal at the participant's wrist could be continuous (i.e., a no gap trial) or interrupted (i.e., a gap trial). When present, the duration of the temporal gap was set at 40 ms for all the three experimental conditions (see Juravle and Spence 2011).

Each trial started with an auditory signal (*start signal*; 50 ms, 400 Hz). This was followed after a random SOA (800–1,200 ms) by a second higher-pitched auditory signal (*go signal*; 50 ms, 800 Hz). Immediately afterward, the tactor that the participants had strapped to their wrist was turned on (2,000 ms, 12 dB sensation level, 250 Hz).

For the *catch condition*, if a temporal interruption occurred in the vibratory stimulus, this could be delivered either in the *preparation* period of the catch movement (10–200 ms after the go signal) or in the *execution* period of the catching movement (700–1,000 ms after the go signal). For gap present trials of the *throw condition*, the gap in the vibration was delivered in the *preparation* period of the throw movement (10–200 ms after the go signal) or during the *execution* of the throw movement (200–700 ms after the go signal). In the control *rest* condition, just as for the experimental conditions, a 2,000 ms vibration was delivered to the participant's wrist. If a gap occurred in the vibratory stimulation, this could be delivered either in the *preparation* period (10–200 ms after the go signal) or in the *execution* period (700–1,000 ms after the go signal). Note that since hand movements were constrained in this condition, the preparation and execution periods are so-called in order to match the experimental catch and throw conditions.

The trial ended with the participants' verbal response regarding the presence versus absence of the temporal gap in the vibration (involving a YES/NO response). The experiment went on to the next trial once the experimenter pressed a key on the keyboard.

Design

Each of the conditions consisted of 2 blocks of 60 trials each, amounting to a total of 360 trials per experiment. The participants were allowed to take short breaks in between the blocks. Half of the trials in each block were GAP trials (the vibration was interrupted very briefly), while the remainder of the trials were NO GAP trials (the vibration was continuous). In half of the GAP trials, the vibration was interrupted in the preparation period, and in the second half, the vibration was interrupted in the execution period. Therefore, the experimental variables were CONDITION (rest, catch, and throw), and TIMING of the gap (gap delivered in the preparation period versus gap delivered in the movement execution period).

Data analysis

For each of the participants, for each of the conditions (rest versus catch versus throw), the percentages of true positives (i.e., YES responses when a gap was present), as well as false positives (i.e., YES responses when a gap was not present) were calculated, split considering the manipulated experimental variable TIMING of the gap (preparation versus execution). These percentages were then normalized and sensitivity measures (d'), as well as criterion c , and relative criterion c' , were derived according to SDT (Green and Swets 1966; Macmillan and Creelman 2005; see Juravle and Spence 2011 for a similar methodology and the equations used to derive the different SDT measures). For those cases in which the accuracy was perfect (i.e., the observed true positives in a proportion of 1), or no false positives were encountered (i.e., 0 false positives observed for an experimental condition), the proportions of 1 and 0 were adjusted 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 assumption of normality was checked with the Kolmogorov–Smirnov test. The normality assumption indicated violations for all levels of the experimental factors, aside from the execution period in both catch and throw conditions (for all tested measures d' , c , and c'), as well as the preparation period in the throw condition (for the d' and c' measures).

Therefore, for each condition (rest, catch, and throw), for each SDT measure (d' , c , and c'), Wilcoxon signed ranks tests (or their parametric equivalent, paired-samples t -tests, if the data were normally distributed) were performed. Furthermore, for each of the SDT measures, one non-parametric repeated measures Friedman's analysis of variance (ANOVA) was conducted on the *preparation* period data with the factor CONDITION (rest versus catch versus throw). Note that we investigated condition effects only for the preparatory period, since the timing of this period was similarly defined for the two movements of interest (i.e., the first 200 ms following the go signal to initiate movement). This ANOVA was followed up with Wilcoxon signed ranks tests in order to investigate differences between the three levels of the tested factor. A Bonferroni correction for multiple comparisons was applied to these post hoc tests; therefore, all effects are reported at a 0.0167 level of significance.

Results

Boxplots of sensitivity and criteria data are presented in Fig. 2.

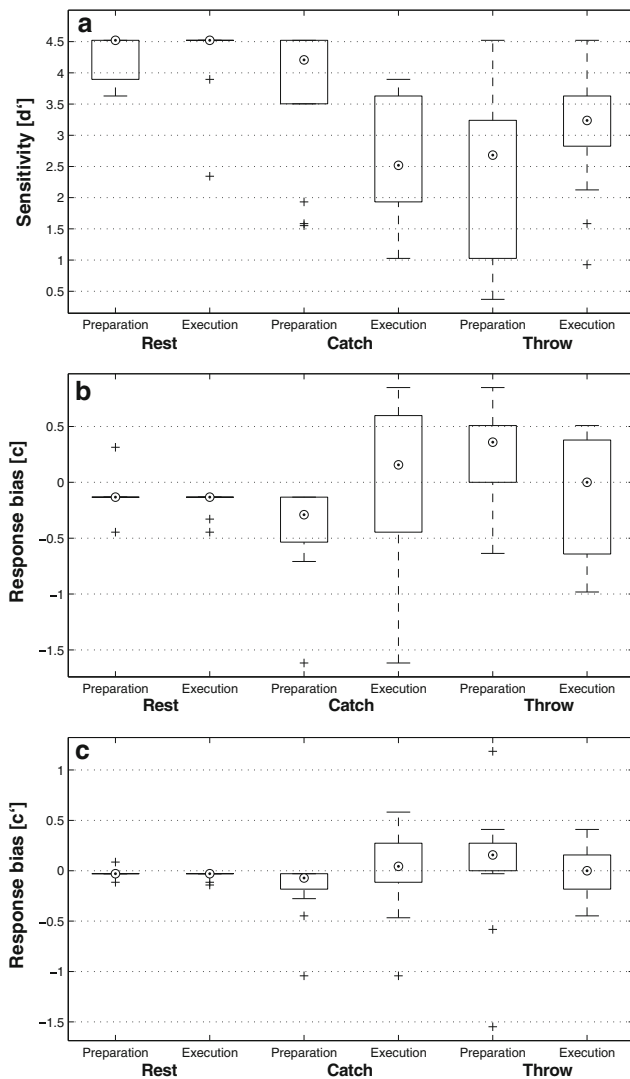


Fig. 2 Boxplots of d' sensitivity data (a), criterion c data (b), and relative criterion c' (c) in Experiment 2, split according to the preparation and execution phases of the movement, for the three conditions (rest, catch, and throw). The box represents the middle 50 % of the data; the whiskers extend to the upper (top 25 %) and lower (bottom 25 %) quartile, respectively; the middle black dot surrounded by a circle denotes the median. Individual data with values higher than 1.5 times the inter-quartiles range are denoted with a plus sign

Sensitivity (d') results

As expected, the results indicated no significant difference between participants' tactile sensitivity in detecting a gap occurring at the beginning (i.e., preparation) or toward the middle (i.e., execution) of the vibratory stimulus [$z = -0.42$, $p = .673$, $r = -0.08$] while at rest. Nevertheless, for the catch condition, a significant difference was observed between the participants' sensitivity to detect a gap in tactile stimulation depending on whether this

appeared in the preparation or the execution period of the movement: That is, participants were significantly more sensitive to the presence of the gap while preparing to catch, as compared to while catching the ball [$z = -2.55$, $p = .011$, $r = -0.48$]. The throw condition indicated an opposite effect [$t(13) = 2.40$, $p = .032$, $r = 0.57$], with participants being significantly more sensitive to detect a gap if this occurred during the actual throwing of the ball, as compared to the preparatory period of the movement.

For the preparation period, the results indicated a significant main effect of condition [$\chi^2(2) = 21.35$; $p < .001$]. Post hoc tests indicated that sensitivity in the preparation period of the throw condition was significantly lower than in both the rest [$z = -3.18$, $p = .001$, $r = -0.60$] and catch conditions [$z = -3.18$, $p = .001$, $r = -0.60$]. Participants' sensitivity in detecting a gap in tactile stimulation did not differ between conditions of rest and preparing to catch a ball [$z = -1.28$, $p = .200$, $r = -0.24$].

For the execution period, the results indicated a decrement in sensitivity for both the catch [$z = -3.97$, $p = .001$, $r = -0.75$] and throw conditions [$z = -3.01$, $p = .003$, $r = -0.56$], as compared to the sensitivity measured in the rest condition.

Criterion c results

The results indicated that for the rest condition, participants' criterion c did not differ for gaps occurring at the beginning (i.e., preparation) or toward the middle (i.e., execution) of the vibratory stimulus [$z = -1.69$, $p = .092$, $r = -0.32$]. However, participants were significantly more inclined to say that there was a gap in the tactile stimulus when this occurred, while they were preparing to catch the ball, as compared to when they were executing the catching movement [$z = -2.27$, $p = .023$, $r = -0.43$]. Conversely, criterion c in the preparation period of the throw condition was significantly more positive, thus showing that participants were more inclined to report that there had not been a gap in the tactile stimulus when this occurred while preparing to throw the ball, as opposed to while executing the throwing movement [$t(13) = 2.50$, $p = .027$, $r = 0.47$].

For the preparation period, the results indicated a significant main effect of condition on the criterion c data [$\chi^2(2) = 19.14$; $p < .001$]. Post hoc tests indicated that in the preparation period participants were more inclined to make a YES response, as compared to both the rest [$z = -2.82$, $p = .005$, $r = -0.53$] and throw conditions [$z = -3.18$, $p = .001$, $r = -0.60$]. Participants' criterion to detect a gap in tactile stimulation differed between conditions of rest and preparing to throw the ball. However, that said, this comparison did not survive the correction for multiple comparisons [$z = -2.27$, $p = .023$, $r = -0.43$].

No significant results were observed for the comparison between rest and execution periods of the two movements.

Criterion c' results

No significant difference was recorded between participants' criterion c' in detecting a gap occurring in the preparatory phase, as compared to the execution phase under conditions of rest [$z = -1.90$, $p = .058$, $r = -0.36$] and throwing [$z = -1.50$, $p = .133$, $r = -0.28$]. However, participants were more inclined to say a gap was present in tactile stimulation when this occurred while they were preparing to catch the ball, as opposed to when they were catching the ball [$z = -2.34$, $p = .019$, $r = -0.44$].

For the *preparation* period, the results indicated a significant main effect of condition on the criterion c' data [$\chi^2(2) = 12.76$; $p = .002$]. Post hoc tests revealed that participants were more inclined to report that a gap was present in the tactile stimulus when this occurred while they were preparing to catch the ball, as opposed to the rest preparation period [$z = -2.82$, $p = .005$, $r = -0.53$]. Participants' criterion c' to detect a gap in tactile stimulation did not differ between the conditions of rest and preparing to throw a ball [$z = -1.43$, $p = .152$, $r = -0.27$]. A comparison of participants' criterion c' between the conditions of preparing to catch and preparing to throw the ball revealed that participants were again more inclined to say a gap was present in stimulation when catching; however, once again, this comparison did not survive the correction for multiple comparisons [$z = -2.13$, $p = .033$, $r = -0.40$].

No significant results were found for the comparison between rest and execution periods of the two movements.

Discussion

In accordance with earlier results, Experiment 2 brings further evidence of a decrement in what is felt over the execution period of a goal-directed movement (Juravle and Spence 2011). However, for the preparation period, as measured here, the SDT results indicate a differential pattern of sensitivity and response bias for self- and externally-generated movements. That is, participants' sensitivity while preparing to throw the ball was significantly lowered, as compared to the rest no-movement condition. Such a result is in line with previous studies indicating that the generation of the motor command is likely to trigger the perceptual attenuation found before the initiation of movement (Chapman and Beauchamp 2006). The same sensitivity decrement was not, however, found for the preparation to catch the ball: In this preparatory phase of the movement, participants' sensitivity remained unchanged, as compared to the rest period.

However, the participants were more inclined to report the presence of a gap in the tactile stimulation, as compared to the rest period. Having found only a decisional decrement in tactile perception for the externally-generated movements—which highlights the lack of involvement of motor-related brain structures in what is felt—made us look for possible explanations of this modulation of tactile perception while preparing an externally-generated movement. As such, a potential explanation could be that while preparing to catch the ball, the participants observed the experimenter's own preparation to throw the ball, which, in turn, triggered this decisional-only decrement in what was felt—participants may have only changed their criterion when judging the presence/absence of a target, but their perceptual sensitivity remained unchanged. Indeed, according to the (mirror neuron) simulation theory for mind-reading (see Gallese and Goldman 1998, for a review), when an observer perceives an actor initiating an action, his motor system should likely mirror-plan the same action.

In Experiment 3, in order to test whether the decrement observed in what is felt results from a change in participants' criterion given that they could potentially plan the experimenter's own movement, we concentrated on the movement preparation phase. For this, in different trials of Experiment 3, the participants were instructed to prepare to catch or throw the ball, or *to observe* the experimenter preparing the same actions. In the observation trials, the participants were only required to perform on the tactile perceptual task; two experimenters were exchanging the ball between themselves, following the auditory signals instructing them to throw the ball. As a baseline control condition, the participants performed the perceptual task at rest. A final aim of Experiment 3 was to investigate whether different postures of the hands give rise to different facilitatory influences from visual attention (Reed et al. 2006). For this, participants' tactile sensitivity was tested in the rest condition not only with their hands at their sides as in Experiment 2 but also with their hands holding the ball at their chest.

Experiment 3

Methods

The methods of Experiment 3 are very similar to that used in Experiment 2, only the differences are highlighted.

Participants

Thirteen participants (5 male, all right-handed) took part in this experiment (mean age of 22 years; age range

18–28 years). The experimental session lasted for approximately 40 min, and the participants received £5 or course credit in return for taking part in the study.

Apparatus and procedure

The apparatus was the same as in the previous experiment. The experimenter's confederate utilized an additional set of headphones. The confederate helped the experimenter during the movement observation blocks. For this, the confederate stood to the participant's left-hand side, approximately one foot away. For the throw observation trials, the experimenter threw the ball at the confederate, who caught it, waited for the end of the trial and participant's verbal response with regard to tactile stimulation, and then returned the ball to the experimenter. For the catch observation trials, the confederate threw the ball to the experimenter, who prepared to catch the ball, caught it, and then returned it to the confederate once the participant had given his/her response for the trial. Note that the participants observed the ball-catching/throwing as performed by the same experimenter, positioned in front of them at a distance of approximately 2.7 meters.

The experiment consisted of six conditions: two control *rest* conditions (hands at sides versus hands on the ball), two *catch* conditions (ball-catching preparation versus ball-catching preparation observation), and two *throw* conditions (ball-throwing preparation versus ball-throwing preparation observation). The experiment was split into 3 parts (rest versus catch versus throw), each consisting of their two corresponding blocks. All of the participants first performed the two blocks of the rest condition. The order of presentation of the experimental (catch and throw) parts of the experiment was counterbalanced across participants. Similarly, the order of the experimental blocks was counterbalanced within each part, across participants. The trial definition and timings were the same as in Experiment 2. Note that in Experiment 3, we only investigated the preparation period of the ball-catching/throwing movements, therefore, when present, the gap in tactile stimulation could occur only within the first 200 ms following the delivery of the go signal indicating that the ball should be thrown.

Design

Each of the experimental parts, as well as the control part, consisted of 2 blocks of 60 trials each, amounting to a total of 360 trials per experiment. Participants were given short breaks in between the blocks. Half of the trials in each block were GAP trials, while the remainder were NO GAP trials. Therefore, the experimental variables were CONDITION (catch versus throw) and TYPE of movement (movement preparation versus movement preparation

observation). The additional rest control condition consisted of two different postures (rest with hands at sides versus rest with hands on the ball).

Data analysis

Just as for Experiment 2, SDT measures were derived for each participant, for each experimental condition. The normality assumption indicated violations for the sensitivity data in the rest (hands on the ball condition) condition.

For each of the SDT measures, in order to investigate within-condition effects, the data were analyzed by means of t-tests/Wilcoxon signed ranks tests. That is, a first group of t-tests was performed in order to compare the two rest, the two catch, as well as the two throw conditions. Furthermore, a second group of t-tests was performed in order to compare the ball-catching/throwing movement types to their corresponding rest posture (hands at sides versus hands on the ball). Lastly, in order to compare the preparation periods of ball-catching and ball-throwing, a 2 CONDITION (catch versus throw) \times 2 TYPE of movement (movement preparation versus movement preparation observation) repeated measures ANOVA was conducted for each of the SDT measures. Significant results were followed up with t-tests. A Bonferroni correction for multiple comparisons was used; the p significance level was set at 0.0125.

Results

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

Sensitivity (d') results

Importantly, no difference was observed between participants' sensitivity across the two rest conditions, with either their hands at the sides or with their hands on the ball [$z = 0.96$, $p = .336$, $r = 0.19$]. Similarly, tactile sensitivity to detect a gap in tactile stimulation did not differ between conditions of preparing to catch the ball and observing the ball being caught [$t(12) = -0.45$, $p = .661$, $r = 0.10$]. Participants' sensitivity was nevertheless lowered when preparing a self-initiated ball-throwing movement, as compared to simply observing the experimenter preparing the same movement [$t(12) = -6.38$, $p < .001$, $r = 0.43$]. Furthermore, when comparing the movement preparation and movement observation conditions to their corresponding rest posture condition, the only significant result was that the participants were less sensitive to detect a gap in tactile stimulation when they prepared a ball-throwing movement, as compared to the rest-hands on the ball condition [$z = -3.19$, $p = .001$, $r = -0.63$].

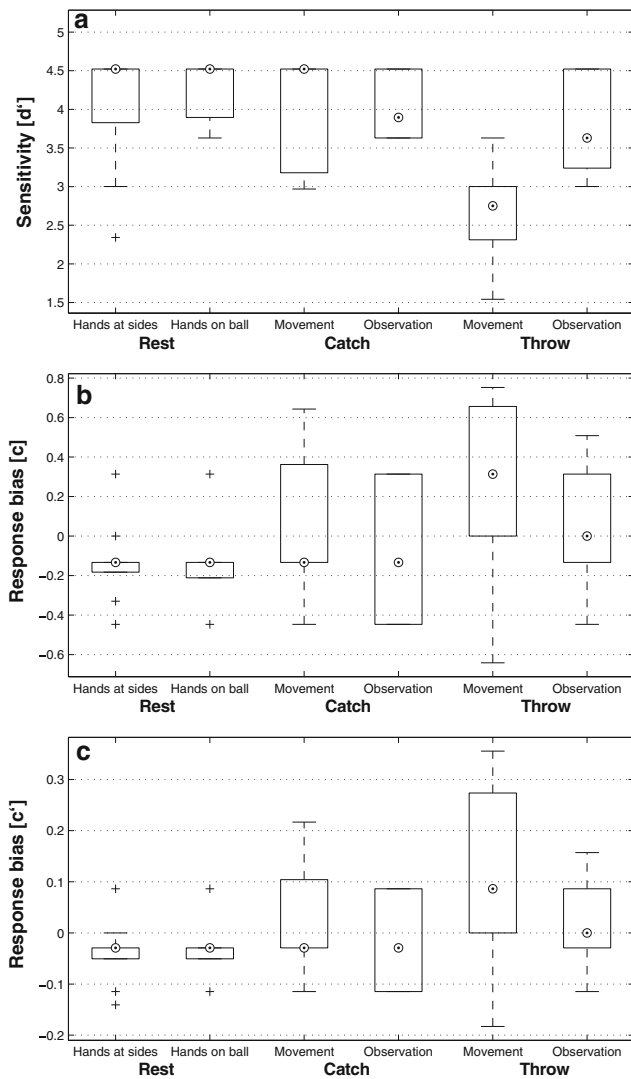


Fig. 3 Boxplots of d' sensitivity data (a), criterion c data (b), and relative criterion c' (c), in Experiment 3, split according to the different hands postures/types of movement preparation, for the three conditions (rest, catch, and throw). The *box* represents the middle 50 % of the data; the *whiskers* extend to the upper (*top 25 %*) and lower (*bottom 25 %*) quartile, respectively; the *middle black dot* surrounded by a *circle* denotes the median. Individual data with values higher than 1.5 times the inter-quartiles range are denoted with a *plus sign*

The analysis of the movement data highlighted main effects of **CONDITION** [$F(1,12) = 29.38$; $p < .001$] as well as of **TYPE** of movement [$F(1,12) = 17.38$; $p = .001$], indicating that participants were significantly more sensitive to detect a gap in tactile stimulation when this occurred while preparing to catch the ball, as compared to ball-throwing. Moreover, their sensitivity was higher when they were simply observing the experimenter preparing to perform the ball-catching/throwing actions, as opposed to their own preparation. Furthermore, a significant 2 **CONDITION** \times 2 **TYPE** of movement interaction

was found in the sensitivity data [$F(1,12) = 13.63$; $p = .003$]. Post hoc investigations indicated that the preparation to throw the ball yielded significantly lower tactile sensitivity as compared to both the preparation to catch the ball [$t(12) = 6.02$, $p < .001$, $r = 0.32$] and the observation of the throwing movement preparation [$t(12) = 6.39$, $p < .001$, $r = 0.43$].

Criterion c results

Participants did not exhibit a significant criterion shift between conditions of rest with their hands at their sides and rest with hands on the ball [$t(12) = 0.41$, $p = .691$, $r = 0.62$], nor did they exhibit a criterion shift between conditions of preparing the ball-catch and observing it [$t(12) = 0.97$, $p = .349$, $r = -0.37$] and preparing the ball-throw and observing it [$t(12) = 1.34$, $p = .205$, $r = -0.13$]. However, when comparing the movement preparation and movement observation conditions to their corresponding rest posture condition, the criterion c results indicated that participants were more conservative in reporting a gap in tactile stimulation when they were preparing to throw the ball [$t(12) = -2.97$, $p = .012$, $r = -0.46$], as well as when only observing the ball-throwing movement preparation from the experimenter's side [$t(12) = -2.79$, $p = .016$, $r = 0.29$], as compared to the rest-hands on the ball condition.

No significant criterion shift was observed when comparing the two movement conditions (catching versus throwing [$F(1,12) = 3.58$, $p = .083$]). Participants were nevertheless more conservative to report a gap for the condition of movement preparation ($M = 0.16$, $SE = 0.05$), as compared to movement preparation observation ($M = 0.01$, $SE = 0.04$, [$F(1,12) = 11.04$; $p = .006$]). Lastly, no significant interaction was observed between the two factors of **CONDITION** and **TYPE** of movement on the criterion c data [$F(1,12) < 1$; n.s.].

Criterion c' results

Participants did not shift their criterion c' between conditions of rest with their hands at their sides and rest with their hands on the ball [$t(12) = 0.02$, $p = .987$, $r = 0.52$], as well as between preparing the ball-catch and observing it [$t(12) = 1.08$, $p = .299$, $r = -0.38$], and preparing the ball-throw and observing the ball-throwing action [$t(12) = 1.90$, $p = .081$, $r = 0.01$]. When compared to the rest-hands at sides condition, participants' criterion c' was significantly more positive in the catch movement preparation (i.e., indicating a conservative shift [$t(12) = -2.33$, $p = .038$, $r = 0.31$]). Moreover, a similar result was found for the ball-throwing preparation criterion c' data: The participants were more conservative in reporting a gap in

the tactile stimulation when they were preparing to throw the ball [$t(12) = -3.02$, $p = .011$, $r = -0.50$], as well as when only observing the ball-throwing movement preparation from the experimenter's side [$t(12) = -2.79$, $p = .016$, $r = 0.29$], as compared to the rest-hands on the ball condition.

The analysis of the movement-only data revealed no significant main effect of CONDITION [$F(1,12) = 4.10$; $p = .066$], as well as no significant interaction between CONDITION and TYPE of movement [$F(1,12) < 1$; n.s.]. However, as revealed by the main effect of TYPE of movement [$F(1,12) = 14.11$; $p = .003$], the participants were more inclined to give a NO response when they prepared the ball-throwing/catching ($M = 0.07$, $SE = 0.02$), as compared to simply observing the experimenter preparing the same action ($M = 0.002$, $SE = 0.01$).

Discussion

Experiment 3 demonstrates that participants' sensitivity and criteria do not change at rest between conditions of keeping their hands at their sides versus keeping their hands on the ball. This result indicates that the possibility that visual spatial attention differentially affecting the different postures of the hands cannot necessarily be taken as a factor explaining the results of Experiment 2. Nevertheless, the motor affordances provided by the different postures of the hands could still have played a role in criterion modulation. Note, for example, that in Experiment 2, participants' criterion c' did not differ between conditions of rest with hands at sides and ball-throwing preparation. However, in Experiment 3, the participants were nevertheless more inclined to give a NO response while preparing the self-initiated ball-throwing movement, as compared to the rest-hands on ball condition. Therefore, it seems that a decisional decrement in what is felt is more likely to be present when similar postures are adopted between movement and nonmovement conditions. That is, we are more likely to experience sensory events related to movement if we have the particular body posture for that movement. This result is important as it has implications for the development of training/rehabilitation programmes for chronic pain patients or for patients recovering from severe brain lesions, such as stroke.

Consistent with the results of Experiment 2, Experiment 3 further supports the existence of a perceptual decrement occurring while preparing a self-initiated movement, as well as the decisional one present for an externally-generated movement. The results of Experiment 3 highlight that not only preparing a self-initiated movement but also, and most importantly, observing an actor preparing such a movement, triggers both perceptual and decisional decrements in what is felt: Participants were more liberal in reporting the presence of a tactile target presented to their

wrists when they were simply *observing* the experimenter preparing the ball-throwing movement. Such a result confirms the main hypothesis of Experiment 3 and demonstrates that decisional changes in tactile perception are triggered by movement observation. These results are further explored in the next section.

General discussion

The present study investigated tactile perception over the time-course of simple throwing and catching movements. The hypothesis was that a differential pattern of tactile sensitivity, together with temporal changes in response bias, would be observed during the various phases of the movements tested. Our results are consistent with previous studies that have highlighted decrements in what is felt during the execution of (self-initiated) goal-directed movements (Buckingham et al. 2010; Gallace et al. 2010; Juravle et al. 2010, 2011), as well as with studies that have documented attenuation for other types of somatic stimuli during self-initiated movements (Helmchen et al. 2006; VanDoorn et al. 2005). Furthermore, our results agree with previous studies that have attempted to explain the attenuation of tactile perception occurring during the motor preparation phase as being the result of the descending motor command (Chapman and Beauchamp 2006). Importantly, the experiments presented here provide new evidence on sensorimotor contingencies and demonstrate that these are differentially taking place over the preparation period of self- versus externally-generated goal-directed movements.

When the ball-catching data in Experiments 2 and 3 are considered in isolation, they indicate that tactile sensitivity in the movement preparation period was unaffected; that is, the participants exhibited comparable levels of performance under conditions of rest and preparing to catch a ball. The participants were nevertheless more biased to report the presence of a gap in the preparation period of the catch, as compared to rest. Thus, during the preparation period of an externally triggered movement a decisional attenuation of tactile perception is observed. This decisional gating of what is felt has even further implications if one considers accounts of tactile gating as just a result of mere action observation (Voisin et al. 2011). As such, even though the participants had not yet initiated their ball-catching movement, they nevertheless still observed the initiation of the throwing action by the experimenter.

This hypothesis was further explored in Experiment 3: Indeed, the mere observation of an actor preparing to execute a (self-initiated) ball-throwing movement triggers a decisional decrement in tactile perception, as highlighted by participants' criterion shift under conditions of action preparation observation in Experiment 3. Observing an

actor preparing a (externally-generated) ball-catching movement does not trigger a criterion shift—participants only exhibit a change in criterion for the observation of self-initiated ball-throwing movements. From this perspective, the decisional-only change observed in our data for the catch trials in Experiment 2, as well as the throw preparation observation in Experiment 3, could be taken to reflect a mirror-like mechanism acting on the motor system during action observation and planning (Gallese and Goldman 1998).

With regard to the ball-throwing data reported in Experiment 2, a pronounced sensitivity decrement was observed during the preparation period of the ball-throwing movement. This result is in line with previous studies that have indicated that additional preparation occurs during the execution of self-initiated movements, as opposed to externally-generated ones (Obhi and Haggard 2004). This result is also in agreement with previous studies highlighting the contribution of the generation of the motor command to the experienced tactile attenuation over the motor preparation phase (Chapman and Beauchamp 2006). For example, triggers for tactile attenuation have been attributed to the primary motor cortex (Voss et al. 2007), as well as the premotor supplementary motor area (SMA, Haggard and Whitford 2004), regions with known involvement in movement planning and generation. Furthermore, the results of Experiment 3 indicate that participants are more conservative when deciding on the presence of a target under conditions of both self-initiated movement preparation and the observation of such movements performed by the experimenter, as compared to a rest condition. When considering these cases of the decisional attenuation of tactile perception, our results suggest that other prefrontal decision-related brain regions are contributing to sensorimotor contingencies. In this respect, previous fMRI studies have already identified the dorsolateral prefrontal cortex to be significantly activated when participants give a correct response in a tactile task (Pleger et al. 2006). Similarly, the premotor pre-SMA was shown to be particularly sensitive in those trials where participants make more false alarms in a tactile task (Conte et al. 2012).

Finally, the most important result to emerge from the present study is highlighted by the comparison between the preparation periods of the two tested movements: catching and throwing. For both movements, the preparation period did not involve any movement of the participant's hands. That is, at the time of the delivery of the gap in tactile stimulation, the goal-directed movement had not yet been initiated, and the participant's hands were thus still at rest. However, if the preparation of the catching movement involved monitoring the experimenter initiating the throw of the ball at most, for the throw movement, the readiness

to move was needed instead. That is, the difference between the two movements can be specified in terms of *the intention* to initiate a goal-directed movement. These results highlight a significant decrement in tactile sensitivity when participants prepared to throw, as compared to when they prepared to catch the ball. This effect was paired in Experiment 2 with a change in response bias (i.e., criterion c response bias: participants were more conservative when reporting a gap in tactile stimulation while preparing to throw, as opposed to preparing to catch). However, when sensitivity differs between experimental conditions, the appropriate measure of response bias is relative criterion c' (Macmillan and Creelman 2005). With this consideration in mind, response bias data as highlighted by this measure were clustered around zero, indicating 'no bias.' Furthermore, no significant difference between the allocation of criterion c' in the two movements' preparatory phases was observed in either Experiments 2 or 3. Therefore, when comparing self- versus externally-generated movements, it appears as though a purely perceptual decline in tactile perception occurs during the preparatory phase of a self-initiated goal-directed movement, and the trigger for this is the intention to execute movement. These results thus hint at a differential involvement of motor and premotor structures during self- versus externally-generated movements.

Taken together, the results of the three experiments reported in the present study therefore provide evidence that different attenuators act on tactile perception, as a result of the preparation to execute a goal-directed movement: If the preparation to perform an externally-generated action (i.e., catching the ball) triggers a decisional attenuation (i.e., participants are more liberal/conservative in reporting a gap in stimulation, as compared to rest), but no change in sensitivity, the preparation to perform a self-initiated action (i.e., the throwing of the ball) triggers a perceptual attenuation (i.e., a participant's sensitivity to tactile stimulation is diminished as a result of, most probably, movement-related gating), together with a conservative change in response bias. These results suggest that sensorimotor contingencies could already be modulated in prefrontal decision-related cortices. Future research needs to address the contribution of prefrontal brain areas to perceptual modulations during goal-directed movement.

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