Anticipatory grasping control modulates somatosensory perception

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Somatosensory perception is hampered on the moving limb during a goal-directed movement. This somatosensory suppression is mostly attributed to a forward model that predicts future states of the system based on the established motor command. Here, we examined whether and how this suppression is modulated by the predictability of object features important for controlling a grasping movement. Participants reached to grasp an object between thumb and index finger and then lifted it as straight as possible. Objects with symmetric or asymmetric mass distributions were presented either in a blocked or random manner, so that the object's mass distribution could be anticipated or not. At the moment of object contact, a brief vibrotactile stimulus of varying intensities was presented on the dorsal part of the moving index finger. Participants had to report whether they detected the stimulus. When the object's mass distribution was predictable, contact points with the object were modulated to the object's centre of mass. This modulation contributed to a minimized resultant object roll during lifting. When the object's mass distribution was unpredictable, participants chose a default grasping configuration, resulting in greater object roll for asymmetric mass distributions. Somatosensory perception was hampered when grasping both types of objects compared to baseline (no-movement). Importantly, somatosensory suppression was stronger when participants could predict the object's mass distribution. We suggest that the strength of somatosensory suppression depends on the predictability of movement-relevant object features.

Introduction

Sensorimotor predictions established by internal forward models are thought to influence the perception of sensory reafferences that are related to the planned movement (Wolpert & Flanagan, 2001). This is traditionally reflected in the hampered perception of self-evoked sensations, such as force production (Shergill, Bays, Frith, & Wolpert, 2003) or self-tickling (Blakemore, Wolpert, & Frith, 2000; Weiskrantz, Eliott, & Darlington, 1971). Nevertheless, externally evoked sensations on the moving limb are also suppressed (Buckingham, Carey, Colino, de Grosbois, & Binstead, 2010; Voss, Ingram, Wolpert, & Haggard, 2008; Voudouris & Fiehler, 2017a; Williams & Chapman, 2002), even if these sensations are not related to a predicted sensory outcome of the action. This points to a rather general somatosensory suppression on the moving limb, which may serve the purpose of releasing capacities to process sensory signals that do not arise on the moving limb and may be more relevant (Gertz, Voudouris, & Fiehler, 2017; Haggard & Whitford, 2004; Voudouris & Fiehler, 2017b; but see also Gertz et al., 2018).

Despite this possible functional role of tactile suppression, this phenomenon remains a rather a paradoxical mechanism, especially when considering that humans need to process sensory feedback from their moving limbs in order to control a movement. Indeed, somatosensory signals for movement control are not only important when they are the sole source of sensory information (Cordo, Carlton, Bevan, Carlton, & Kerr, 1994), but also when online visual feedback is available (Oostwoud-Wijdenes, Brenner, & Smeets, 2011; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Voudouris, Smeets, & Brenner, 2013). Moreover, when the moving hand is insensitive to proprioceptive or tactile afferences, reaching and grasping movements become more variable and take longer (Gentilucci, Toni, Chieffi, & Pavesi, 1994; Gentilucci, Toni,

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Daprati, & Gangitano, 1997; Ghez, Gordon, & Ghilardi, 1995; Gordon, Ghilardi, & Ghez, 1995; Johansson & Flanagan, 2008; Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006). Therefore, hindered somatosensory processing during movement seems to be suboptimal as it hampers the synthesis and utilization of movement-relevant sensory signals.

In fast feedforward movement control, when open loop policies dominate, lack of somatosensory input may not pose serious problems to the executed movement (Messier, Adamovich, Berkinblit, Tunik, & Poizner, 2003; Rothwell et al., 1982). Similarly, in well-predictable environments, when the imposed movement demands can be predicted, online somatosensory signals may not be particularly essential, as all the necessary input is available for successful movement control (Rand, Shimansky, Stelmach, & Bloedel, 2004; Wilmut & Barnett, 2014). For instance, when reaching to grasp objects of different heights, humans choose contact points that are closer to the object's center of mass already before moving to those points (Voudouris, Brenner, Schot, & Smeets, 2010). Moreover, when grasping an object with a known asymmetric mass distribution, humans choose appropriate contact points to avoid disturbing the object's equilibrium after the grasp (Fu, Zhang, & Santello, 2010; Lukos, Ansuini, & Santello, 2007). On the other hand, when external changes during a movement occur, somatosensory afferences are critical for reactive motor adjustments (Aivar, Brenner, & Smeets, 2008; Day & Lyon, 2000; Voudouris et al., 2013). In such scenarios with high sensory uncertainty, suppression of somatosensory signals from the moving limb may be a suboptimal strategy for successful movement control as it impairs continuous monitoring of sensory feedback. For instance, when grasping and lifting objects of unknown mass distributions, humans choose contact points that allow compensatory torques to all possible object imbalances after the grasp (Lukos et al., 2007). The need for sensorimotor flexibility may have important implications on the function and regulation of somatosensory suppression during movement.

Here we examined whether and how the predictability of movement-relevant object features modulates somatosensory perception during movement. For this reason, we asked participants to grasp and lift as straight as possible an object that had either a predictable or an unpredictable mass distribution. Following previous work (Fu et al., 2010; Lukos et al., 2007), we hypothesized that for objects with predictable properties participants would tailor their contact points such that object roll during lifting would be minimized. For objects with unpredictable mass distribution, we hypothesized that participants would choose contact points that would provide maximal flexibility for lifting the object. To probe somatosensory suppression, we presented a brief vibrotactile stimulus on the index finger of the right grasping hand at the moment of contact with the object. Based on previous findings (Buckingham et al., 2010; Fraser & Fiehler, 2018; Voudouris & Fiehler, 2017a), we expected somatosensory suppression during movement (i.e. that somatosensory sensitivity would deteriorate during grasping compared to rest). Importantly, if somatosensory suppression would be modulated by the predictive power of the forward model, we expected stronger suppression when the object's mass distribution was predictable than when it was unpredictable.

Methods

Participants

Twenty-four participants (17 women, 7 men; aged 20–56 years, with median age of 24 years) joined the experiment. They were all right-handed according to the Edinburgh Handedness Inventory (88 ± 3; Oldfield, 1971) and had normal or corrected-to-normal vision. They were compensated with 8€/hour or with course credits for their efforts. The study was approved by the local ethics committee and was in accordance with the Declaration of Helsinki (2008).

Apparatus

Participants sat comfortably in front of a table (118 × 80 cm). They wore liquid-crystal shutter glasses (PLATO, Translucent Technologies, Toronto, Canada) and over-ear headphones, through which white noise was played at a comfortable volume throughout the experiment. The noise served the purpose of masking any sounds related to changing the object's mass distribution between trials and to the presence or absence of a vibrotactile stimulus. Participants started each grasping movement from a start position ~30 cm in front of their body and aligned to their right shoulder. They had to reach and grasp an object placed at one of two lateral positions, each located 34 cm away from the start position. We used two different object positions to avoid stereotyped movements. The object had an inverted T-shape and was made of polyoxymethylene (156 g). Its lower part had a width of 15 cm and a height of 3 cm, while its upper part had a width of 5 cm and a height of 7 cm. Its depth (5 cm) was the same for both parts. At the backside of the object, three tubes (2 cm in diameter, 4.5 cm in depth) were distributed laterally. In each trial, one of these tubes was filled with a piece of brass (~2 cm in diameter; ~4.5 cm in depth; 117 g), creating a symmetric or

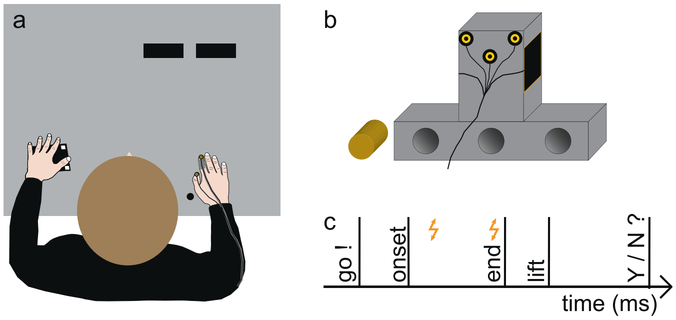

Figure 1. (a) Top view of the setup with the start position (circle) and the two possible object positions (rectangles) drawn. (b) Illustration of the backside of the object with the three infrared markers fixed to it. The left touch sensor is visible. The three tubes within the object's base and the piece of brass are also depicted. (c) Timeline of a single grasping trial with the flash symbols illustrating the moments of stimulations (500 ms after the go-cue; at the moment of the grasp).

asymmetric mass distribution. Four round pieces of felt pad were attached to the corners of the object's base of support to eliminate any possible auditory cues when placing the object on the table. The total mass of the object together with the brass was 273 g. An illustration of the setup and the object is depicted in Figure 1.

A touch sensor (4.37 × 4.37 cm; Interlink Electronics Inc., Westlake Village, CA) was attached on each grasping side of the upper part of the object. These sensors were connected through a NI USB-6009 device (National Instruments Corporation, Austin, TX) to the host PC and recorded the moment of the touch to trigger a vibrotactile stimulation in the respective trials.

Vibrotactile stimuli (250 Hz, 25 ms) were presented on the dorsal part of the participants' right index fingers through a vibrotactile stimulation device (Engineering Acoustics, Inc., Casselberry, FL). The stimuli were presented either shortly after movement onset (500 ms after an auditory go-cue) or at the moment of contact with the object. Stimuli had variable intensities with a peak-to-peak displacement that ranged from 9.4 to 56.7 μm in steps of 9.4 μm, while 25% of the trials involved no stimulation.

The positions of five infrared markers were recorded at 100 Hz with an Optotrak Certus motion tracking system (Northern Digital, Inc., Waterloo, ON, Canada). Two small infrared markers were attached to the participants' right thumb and index fingernails. The marker on the index finger was housed in a custom-made pyramid case (1 × 1 × 1 cm) to facilitate its visibility from the camera. Three markers were attached in a triangular configuration to the backside of the object. Care was taken that all cables from the devices did not hinder the participants' movements or the way the object could be grasped.

Procedure

Participants performed five blocks of trials: one baseline block and four grasping blocks. The baseline block comprised only the tactile detection task. Each of the four grasping blocks comprised the tactile detection task during a grasping movement. In three of the grasping blocks participants grasped an object that had a predictable mass distribution (predictable left, predictable center, predictable right) throughout that block. In the fourth block, the object had an unpredictable mass distribution in every trial.

In the baseline block, participants placed their right hand in a comfortable configuration in front of them. Vision was allowed during the whole block. A vibrotactile stimulus was presented in the beginning of each trial. An auditory cue was presented 700 ms after the stimulus, prompting participants to indicate whether they had felt a stimulus or not by pressing a button with their left hand. The next trial started 500 ms after the participants' response. We presented 5 trials for each stimulus intensity and 10 no-stimulation trials, resulting in a total of 40 trials. The baseline block lasted approximately 2 minutes.

Before each grasping block, participants performed eight practice trials, all with the same mass distribution that they would experience during the upcoming block, while the object's position was being counterbalanced. Participants were explicitly told that the mass distribution during the upcoming grasping block would be the same as during the practice trials.

In each grasping block, participants placed their right hand on the start position with their thumb and index finger touching each other. While the shutter glasses were opaque, the experimenter placed the object with the appropriate mass distribution at its appropriate position. An auditory cue, presented after the shutter glasses turned transparent, notified participants that they could start their reach-to-grasp movement. They had to grasp the object from its long sides with a precision grip, with the thumb and index finger on the sides where the touch sensors were attached. After grasping the object, participants were instructed to lift it as straight as possible for ~10 cm before placing it back to its original position and returning their hand back to the start position. The shutter glasses would then turn opaque, and an auditory cue would inform participants that they had to respond whether they had felt a vibrotactile stimulus during the trial by pressing a button with their left hand.

In each of the three predictable grasping blocks, the object's mass distribution remained the same throughout the block, being either symmetric, or asymmetric to the participant's left or right. In each of these blocks, we presented 5 trials for each stimulus intensity and 10 no-stimulation trials at the moment of contact as determined by the touch sensors. One trial for each stimulus intensity and two no-stimulation trials were also presented earlier in the movement (500 ms after the go-cue) to decrease participants' expectations of a stimulus at the moment of contact with the object. This resulted in a total of 48 trials, with 24 trials having the object on the left and the other 24 trials on the right position. Each predictable block lasted approximately 6 minutes.

In the unpredictable block, the experimenter changed the mass distribution in each trial on a pseudorandomized order while the shutter glasses were opaque. Even when two consecutive trials involved the same distribution, the experimenter still pulled out and inserted the brass so that participants could not predict where the mass was inserted, in case they could hear this despite the white noise. Each of the three mass distributions was presented 48 times, as in the predictable blocks, resulting in a total of 144 trials. The unpredictable block lasted approximately 20 minutes.

The three predictable grasping blocks were presented in a row to engage participants in a strong predictable procedure, while the order of these blocks was counterbalanced across participants. The unpredictable block was presented either before or after the three predictable blocks, while the baseline block was presented either before or after the grasping blocks. The presentation of these blocks was also counterbalanced across participants.

Data analysis

We first examined whether the manipulation of the predictability of the object's mass distribution influenced the participants' kinematic behavior. Here, we focused on the placement of the digits on the object depending on the mass distribution (Lukos et al., 2007). To do so, we first determined the three-dimensional velocity of the hand by numerical differentiation of the average position of the infrared markers on the two digits. Movement onset was defined as the first of five consecutive frames (50 ms) with a velocity greater than 20 cm/s. We then determined movement end for each digit separately; this was defined as the first frame after movement onset in which the velocity of the digit dropped back below 10 cm/s. *Digit separation* was the difference in the digits' vertical positions at the moment of each digit's contact, with positive values representing the thumb being higher than the index finger. We also calculated *object roll* as the angle between the table and the markers on the object, with 0° values representing that the object was lifted straight up, and positive values representing that it rolled to the right (from the perspective of the participant). We calculated the maximal object roll for the time period from the onset of the object's lift until 250 ms after (cf., Fu et al., 2010). Lastly, *loading time* was the time difference between the earliest endpoint and the beginning of the object lift, which was defined as the first frame in which the markers on the object exceeded a vertical velocity threshold greater than 20 cm/s. The values of the above-mentioned kinematic variables were calculated for each trial of each of the four grasping blocks and were then averaged across the repetitions of each participant. We submitted the above-mentioned variables to a 3 (left, center, right) × 2 (predictable, unpredictable) repeated measures ANOVA. Interactions between the factors were further investigated with separate one-way ANOVAs for the two predictability conditions. Significant differences between the conditions were examined with Bonferroni-corrected two-tailed post hoc *t* tests (corrected $\alpha = 0.016$).

For the perceptual behavior, we fitted the detection responses for stimuli at the moment of object contact to a logistic function using the maximum-likelihood estimation within the MATLAB (MathWorks, Natick, MA) psignifit toolbox (Wichmann & Hill, 2001). The detection threshold was calculated as the 50% of the psychometric function, and the detection precision was calculated as the difference between the 50% and the 84% of the function, which corresponds to one standard deviation of the Gaussian distribution. To quantify the effect of prediction on somatosensory perception, we subtracted each participant's baseline detection threshold and precision from his or her respective values in each of the grasping blocks. This resulted in two relative measures ($\text{detection}_{\text{diff}}$, $\text{precision}_{\text{diff}}$) with higher positive values representing stronger somatosensory suppression. We calculated each of these values for each of the four measured blocks (predictable left, predictable center, predictable right, unpredictable) for each participant, and then averaged them for each block across the participants. First, we wanted to confirm that we do find the expected somatosensory suppression during movement (Gertz et al., 2017; Voudouris & Fiehler, 2017a). To do so, we examined the effect of the grasping movement on somatosensory perception by testing the $\text{detection}_{\text{diff}}$ and $\text{precision}_{\text{diff}}$ of each block against zero by using two-sided paired *t* tests (corrected $\alpha = 0.01$). In a second step, we investigated whether somatosensory suppression was influenced by the object's mass distribution depending on its predictability. To this end, we sorted the trials of the unpredictable block by mass distribution (unpredictable left, unpredictable center, unpredictable right) and then calculated $\text{detection}_{\text{diff}}$ and $\text{precision}_{\text{diff}}$ separately for each of these three distributions. We then performed a 3 (left, center, right) × 2 (predictable, unpredictable) repeated measures ANOVA separately for $\text{detection}_{\text{diff}}$ and $\text{precision}_{\text{diff}}$. Interactions between the factors were further investigated with separate one-way ANOVAs for the two predictability conditions, and significant differences between the conditions were examined with two-tailed post hoc t tests (Bonferroni-corrected; $\alpha = 0.016$).

Participants with a detection threshold beyond the stimulus range in any of the predictable-all (see Results) or unpredictable grasping blocks were excluded from further perceptual and kinematic analysis. We also excluded one participant due to failure in the data acquisition. This resulted in a total of 20 participants in our final sample. Trials of those 20 participants, in which the endpoint of one of the digits was detected as being after object lift, were excluded from the kinematic analyses (16.2%).

Results

Participants placed their digits on the object differently in the two predictability conditions, $F(1, 19) = 5.9$, $p = 0.024$, $\eta^2 = 0.24$ (Figure 2a), as digits' separation was negligibly greater in the unpredictable than the predictable condition (mean ± standard deviation: 0.5 mm ± 4 mm). We also found an effect of the object's mass distribution, $F(2, 38) = 32.3$, $p < 0.001$, $\eta^2 = 0.63$): the further the mass was distributed to the left, the greater was the digits' separation. However, the effect of mass distribution on digits' separation depended on the predictability, $F(2, 38) = 36.2$, $p < 0.001$, $\eta^2 = 0.66$: participants tailored their endpoints' in the predictable, $F(2, 38) = 36.6$, $p < 0.001$, $\eta^2 = 0.66$, but not in the unpredictable condition, $F(2, 38) = 1.6$, $p = 0.199$, $\eta^2 = 0.08$. More specifically, in the predictable condition, the mass distributions significantly differed from each other showing the largest digits' separation when the mass was distributed to the left and the smallest when it was distributed to the right (all $t > 4.1$, all $p < 0.001$, all Cohen's $d > 0.86$). Note that digits' separation reflects the difference in the position of the markers on the fingernails and not of the fingertips, and that the digits' separation when grasping asymmetric objects is symmetrically modulated with respect to the symmetric object. In sum, being able to establish predictions about the object's mass distribution modulated the chosen endpoints on the object.

Object roll was influenced by the object's mass distribution, $F(2, 38) = 195.6$, $p < 0.001$, $\eta^2 = 0.91$ (Figure 2b): the further the mass was distributed to the left, the smaller was the object roll. Most importantly, there was a significant interaction between predictability and mass distribution, $F(2, 38) = 105.3$, $p < 0.001$, $\eta^2 = 0.84$. Mass distribution influenced object roll in both the predictable, $F(2, 38) = 103.3$, $p < 0.001$, $\eta^2 = 0.84$, and the unpredictable condition, $F(2, 38) = 196.4$, $p < 0.001$, $\eta^2 = 0.91$, but this influence was weaker in the predictable condition. More specifically, objects with asymmetric mass distributions rolled less in the predictable than the unpredictable condition (left: $t_{19} = 10.7$, $p < 0.001$, Cohen's $d = 2.21$; right: $t_{19} = -8.4$, $p < 0.001$, Cohen's $d = 1.55$). There was no difference between the conditions for the symmetric mass distribution ($t_{19} = 1.2$, $p = 0.216$, Cohen's $d = 0.23$). In short, object roll was much smaller when participants could anticipate its mass distribution.

Loading times were influenced by the predictability of the object's mass distribution, $F(1, 19) = 19.8$, $p < 0.001$, $\eta^2 = 0.51$ (Figure 2c): participants took longer to start lifting the object when they could not predict its mass distribution. There was no main effect of the object's mass distribution, $F(2, 38) = 1.2$, $p = 0.308$, $\eta^2 = 0.06$, nor any interaction, $F(2, 38) = 1.6$, $p = 0.209$, $\eta^2 = 0.08$. As the object had always the same mass, these longer loading times may reflect different operations, such as longer processing times to compensate for the uncertain mass distribution, or to build up appropriate forces or even effects of the distribution experienced in the previous trial (cf., Lukos, Choi, Santello, 2013).

The kinematic results show that movements towards objects with predictable mass distribution were planned

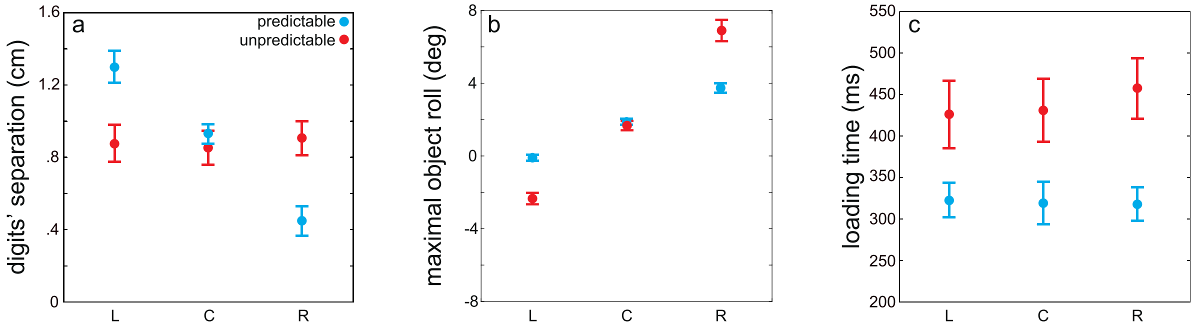

Figure 2. Kinematic results. (a) Digits' separation at the moment of contact, (b) maximal object's roll during the first 250 ms after object lift, and (c) loading time. Each pair of data in each panel shows results for the left (L), center (C), and right (R) mass distributions for the predictable (cyan) and unpredictable (red) blocks. Average values with error bars indicating the standard error across the participants' means.

in a feedforward manner: participants tailored their digit configuration at the moment of contact and successfully minimized object roll, a strategy that can only result from predictive mechanisms. Due to the stronger feedforward control in the predictable than unpredictable blocks, we also expect stronger somatosensory suppression when the mass distribution is known.

Figure 3a shows the psychometric functions of a representative participant for the predictable and unpredictable blocks. In line with previous studies (Colino & Binsted, 2016; Gertz et al., 2018; Voudouris & Fiehler, 2017a), somatosensory perception was deteriorated in grasping blocks compared to baseline, as this was reflected in elevated detection thresholds in the predictable left ($t_{19} = 4.6$, $p < 0.001$, Cohen's $d = 1.04$), predictable center ($t_{19} = 4.8$, $p < 0.001$, Cohen's $d = 1.07$), predictable right ($t_{19} = 4.7$, $p < 0.001$, Cohen's $d = 1.05$), and unpredictable blocks ($t_{19} = 6.6$, $p < 0.001$, Cohen's $d = 1.48$; Figure 3b). Detection precisions did not differ from baseline, all $t < 2.3$, all $p > 0.028$ (corrected $\alpha = 0.01$), all Cohen's $d < 0.53$; Figure 3c). In short, tactile stimuli were suppressed in both the predictable and unpredictable blocks as compared to the baseline.

Detection thresholds were greater in the predictable than unpredictable conditions, $F(1, 19) = 5.6$, $p = 0.028$, $\eta^2 = 0.23$; Figure 3b). There was no main effect of the object's mass distribution, $F(2, 38) = 2.2$, $p = 0.117$, $\eta^2 = 0.11$, but we found an interaction between predictability and mass distribution, $F(2, 38) = 3.6$, $p = 0.036$, $\eta^2 = 0.16$: detection thresholds were influenced by the mass distributions in the predictable, $F(2, 38) = 3.2$, $p = 0.050$, $\eta^2 = 0.14$, but not in the unpredictable condition, $F(2, 38) = 1.8$, $p = 0.174$, $\eta^2 = 0.08$. In the predictable condition, however, post hoc t tests did not reveal any significant difference between the three mass distributions, all $t < 2.2$, all $p > 0.041$ (corrected $\alpha = 0.016$), all Cohen's $d < 0.48$.

In line with the effects on detection thresholds, being able to predict the object's mass distribution deteriorated the detection precision, $F(1, 19) = 19.1$, $p < 0.001$, $\eta^2 = 0.50$; Figure 3c). There was no main effect of the mass distribution, $F(2, 38) = 1.7$, $p = 0.192$, $\eta^2 = 0.08$, or an interaction between predictability and mass distribution, $F(2, 38) = 2.1$, $p = 0.148$, $\eta^2 = 0.09$.

To validate the effects of predictability on somatosensory suppression, we also merged the detection responses of the three predictable blocks to a new, unified block (predictable-all), for which we estimated new detection$_{\mathrm{diff}}$ and precision$_{\mathrm{diff}}$ values. This had the advantage of estimating perceptual responses with the maximal possible number of trials, as we did in the unpredictable block. Based on the main effects we found before, we hypothesized that suppression is more pronounced in the predictable than unpredictable condition. Hence, we compared detection$_{\mathrm{diff}}$ and precision$_{\mathrm{diff}}$ between the predictable-all and the complete unpredictable block using a one-sided paired t tests ($\alpha = 0.05$). The results corroborated our previous findings: detection thresholds deteriorated in the predictable-all than the unpredictable block ($t_{19} = 2.4$, $p = 0.012$, Cohen's $d = 0.51$; rightmost data in Figure 3b), and so did detection precision ($t_{19} = 1.8$, $p = 0.041$, Cohen's $d = 0.59$; rightmost data in Figure 3c). These results show that the predictability of grasp-relevant object features modulate somatosensory suppression (i.e., somatosensory perception deteriorates more when stronger sensorimotor predictions are established).

Because the precision of sensorimotor predictions plays a central role in determining the strength of somatosensory suppression (Blakemore, Frith, & Wolpert, 1999), we further examined if participants who established stronger predictions also showed stronger suppression. To do so, we explored whether

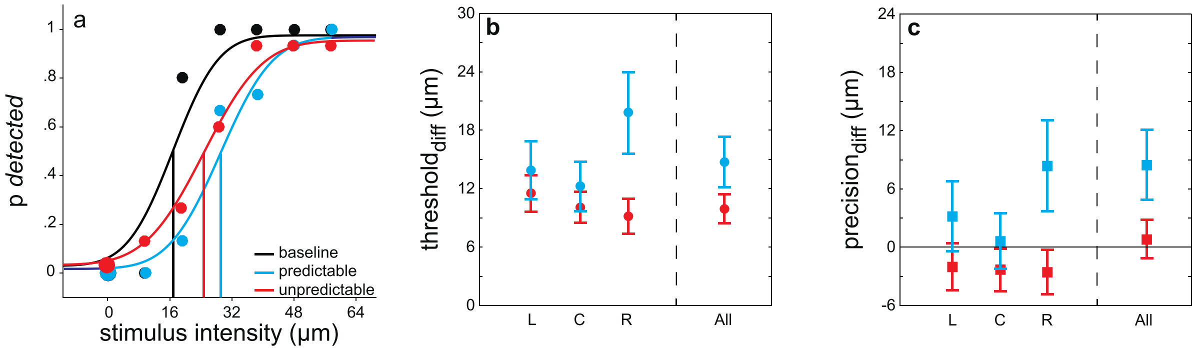

Figure 3. (a) Psychometric functions of a representative participant for the baseline, predictable and unpredictable blocks, differences in (b) detection thresholds, and (c) detection precisions between grasping and baseline blocks. The first three pairs of data in panels b and c show results for the left (L), center (C), and right (R) mass distributions for the predictable (cyan) and unpredictable (red) blocks. The last pair (All) in these panels shows data for the predictable-all and the unpredictable blocks. Zero values represent no change from baseline, while positive values represent suppression in the grasping blocks. Details as in Figure 2.

each participant's strength of suppression in the predictable-all block is correlated with the separation of the digits' endpoints in the same block, bearing in mind that the separation of the digits is not the sole indicator of anticipatory control of grasping, as digit forces contribute as well (Lukos et al., 2013). We found no correlation between detection thresholds and digits' separation ($r = -0.37$, $p = 0.108$). Moreover, we explored whether suppression decreased when longer loading times were observed. Again, no correlation was found between somatosensory suppression in the predictable-all block and the loading time ($r = 0.21$, $p = 0.336$).

Discussion

In this study, we examined whether the ability to accurately predict the sensorimotor demands when grasping an object modulates the strength of somatosensory suppression. We show that when grasping and lifting an object with a predictable mass distribution, participants were able to anticipatorily choose appropriate contact points in order to minimize object roll. On the contrary, when grasping an object with an unpredictable mass distribution, participants opted for "default" contact points, a strategy that resulted in excessive roll when lifting it. These results demonstrate that participants were able to accurately predict the sensorimotor demands during the upcoming lifting action of an object with predictable mass distribution and thereby optimally tailor their contact points. Meanwhile, somatosensory perception during grasping was hampered compared to a situation in which no movement was performed, which is in line with previous findings (Buckingham et al., 2010; Voudouris & Fiehler, 2017a). Importantly, this somatosensory suppression was stronger when grasping an object with a predictable than an unpredictable mass distribution. This suggests that somatosensory suppression increases when people can accurately predict the sensorimotor demands of the upcoming movement.

The contact points clearly depended on the predicted mass distribution reflecting the predictive mechanism involved in grasping control. The difference in height between the contact points was at its extremes for the two asymmetric, predictable mass distributions. That participants tailored their contact points in a predictive manner does not come as a surprise considering that anticipatory planning is evident in many stages of a grasping movement. For instance, humans choose suitable contact points for different objects before moving toward those points (Roche, Verheij, Voudouris, Chainay, & Smeets, 2015; Voudouris et al., 2010). Depending on the subsequent manipulation, humans also select a comfortable or awkward end posture (Rosenbaum & Jorgensen, 1992), and they shape their grip accordingly while they are reaching for the object (Ansuini, Santello, Massaccesi, & Castiello, 2006). Our current finding that contact points are tailored to the object's mass distribution is in line with previous work (Fu et al., 2010; Lukos et al., 2007), and confirms that feedforward processes play a key role in grasping control.

Feedforward control during hand movements results in the well-established phenomenon of somatosensory suppression (Blakemore et al., 2000; Buckingham et al., 2010; Fraser & Fiehler, 2018; Voudouris & Fiehler, 2017a). The precision with which one can establish such sensorimotor predictions has a central role on the modulation of somatosensory suppression (Blakemore et al., 1999). Accordingly, our present results show that somatosensory suppression is stronger when planning and performing a grasping movement that is strongly predictive in nature. Yet, feedback signals at the moment of contact arising from the moving hand may modulate somatosensory processing. More specifically, when grasping an object with an unpredictable mass distribution, it would be advantageous to estimate its mass distribution before lifting it (e.g., during the loading time) to minimize its roll. In the absence of visual cues (e.g., when not being able to see the loading pattern of an object), feedback signals from the hand after object contact and before object lift (during the loading time) are the sole source of information about the object's mass distribution. The longer loading times that we found in the unpredictable condition might point to the idea that participants processed afferent signals to estimate the object's mass distribution to accordingly tailor their forces. Our results are inconsistent with findings of Lukos et al. (2007) and Lukos, Dongpyo, Poizner, & Santello (2010) who showed shorter loading times for objects with unpredictable than predictable mass distributions. However, because we still observed greater object roll in the unpredictable than predictable condition, the possibility that longer loading times provided additional afferent information about the object's mass distribution is unlikely, and even if, it could not counteract the lack of strong predictions about the mass distribution. Instead, it is more likely that the increased loading times in the unpredictable condition are caused by other factors, such as building-up of stronger vertical forces (Brenner & Smeets, 1996; Gordon, Forssberg, Johansson, & Wrestling, 1991) due to suboptimal digit placement, or anticipatory effects based on the mass distribution experienced in the previous trial (Lukos et al., 2013).

Suppression seemed slightly stronger when grasping an object with a predictable mass distribution to the right. When grasping to lift objects of asymmetric mass distributions while digit placement is unconstrained, people adjust both their contact points and their applied digit forces to minimize object roll (Lukos et al., 2013). Of course, when digit placement is constrained, people can only adjust the applied forces (Fu et al., 2010). In the current study, participants separated their digits much less than the size of the 4 × 4 cm touch sensors allowed (Figure 2a). Therefore, asymmetric objects may not have led only to the adjustment of contact points, but also of the applied forces, as has been shown in previous work (Lukos et al., 2013). In this case, the detection of tactile stimuli may be even more hampered because sensorimotor noise on the digit that exerts stronger force is expected to increase (Harris & Wolpert, 1998). For objects with mass distributions to the right, the index finger may have applied greater forces to counteract the object's roll. Because we probed somatosensory sensitivity on this digit, stronger forces might explain this apparent stronger suppression in that configuration.

To conclude, our results show that the strength of somatosensory suppression during movement depends on the predictability of movement-relevant object features. This suggests that predictions established in feedforward control influence the strength of somatosensory suppression.

Keywords: tactile perception, tactile suppression, contact points, prediction

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