Illusory tactile movement crosses arms and legs and is coded in external space

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Abstract

Humans often misjudge where on the body a touch occurred. Theoretical accounts have ascribed such misperceptions to local interactions in peripheral and primary somatosensory neurons, positing that spatial-perceptual mechanisms adhere to limb boundaries and skin layout. Yet, perception often reflects integration of sensory signals with prior experience. On their trajectories, objects often touch multiple limbs; therefore, body-environment interactions should manifest in perceptual mechanisms that reflect external space.

Here, we demonstrate that humans perceived the cutaneous rabbit illusion – the percept of multiple identical stimuli as hopping across the skin – along the Euclidian trajectory between stimuli on two body parts and regularly mislocalized stimuli from one limb to the other. A Bayesian model based on Euclidian, as opposed to anatomical, distance faithfully reproduced key aspects of participants' localization behavior.

Our results suggest that prior experience of touch in space critically shapes tactile spatial perception and illusions beyond anatomical organization.

Introduction

Our everyday life is defined by interactions between the body and the environment. Action and perception work together to create a loop: we perceive to act and act to perceive (Ernst & Bülthoff, 2004; Friston, 2010; Gibson, 1966, 1979; Neumann & Prinz, 1990; Witt & Riley, 2014; Wolpert & Ghahramani, 2000). Through this loop, our perception of the world and of our own body in space is shaped by experience. The brain interprets incoming sensory input and employs assumptions, or expectations, to compensate for uncertainty that is due to sensory noise. The resulting percept is often a compromise between the actual sensory input and experience-based expectations (Goldreich, 2007; Goldreich & Tong, 2013; Körding & Wolpert, 2004; Shams & Beierholm, 2010). The compromise between sensory input and expectation can evoke perceptual illusions, which usually express the brain's expectations overriding sensory mismatch (e.g. Brown et al., 2013; Hayward, 2015). For instance, touch is not always perceived at its true location but is ascribed elsewhere to better "fit" with a perceptual expectation.

The famous cutaneous rabbit effect is a prime example of a perceptual illusion: A rapid sequence of stimuli, presented at two positions on the skin several centimeters apart, evokes the percept of a stimulus sequence that gradually moves along the stretch of skin between the truly stimulated positions (e.g. Geldard & Sherrick, 1972; Trojan et al., 2010). A common explanation for this percept is that it arises from the brain's assumption that stimuli that occur close to each other in time and space originate from one common source (Goldreich, 2007; Goldreich & Tong, 2013; Tong et al., 2016); in the case of the cutaneous rabbit, the common source may be a hypothetical rabbit that hops across the skin, giving the illusion its name. This idea is elegantly captured by a Bayesian observer model that posits that the brain uses a low velocity prior, that is, a generalized expectation that successive stimuli are caused by a common object that moves continuously along the skin at a speed typically encountered in real life. The model gives higher relative weight to the prior the higher spatial uncertainty about the sensory input is, which can ultimately result in a percept that reflects previous experience more than the present input.

How could a prior favoring the rabbit-like percept arise? On many occasions, we perceive things moving along the skin, creating an orderly sequence of tactile input. Every occurrence of a moving object along the skin updates and strengthens the brain's expectation that this type of stimulation pattern is caused by one common, persistent object. Some studies, especially in the visual modality, have shown that exposure to altered rules, such as stimulus probabilities and the contingency between different sensory inputs, change our perceptual priors (Adams et al., 2004; Barnett-Cowan et al., 2018; Di Luca & Rhodes, 2016). For instance, visual patches are typically perceived as convex when they are brighter on the top half. Yet, this judgment can change with visuo-haptic training, with participants effectively modifying their "light-from-above" prior (Adams et al., 2004). Generally, then, experience-shaped priors reflect stimulation patterns that arise from regularities in the world, such as how our body in space normally encounters moving objects.

Critically, the use of external space within the framework of moving objects is not straightforward in the tactile system. Our tactile sensors lie in the 2D sheet that is our skin, and this anatomically-based 2D reference frame must be converted into an external reference frame

that reflects where the touch happened in space. This transformation entails combining skin location with posture, and, when an object moves across several body parts, taking into account the spatial relationships between them (Heed et al., 2012; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Hence, anatomical **and** external space are firmly linked in the tactile system (for review see Badde & Heed, 2016; Longo et al., 2010; Medina & Coslett, 2010; Tamè et al., 2019).

Given the central role of spatial priors in the Bayesian observer model and given that these priors reflect previous experience gained through environmental interactions – that is, interactions that take place in external space –, it may strike as surprising that, until now, the model has always been applied to anatomical space. Similarly, explanations of the cutaneous rabbit effect have almost exclusively focused on the illusion as a phenomenon related to anatomical, and not to external spatial processing. For example, early studies proposed low-level interactions in the skin and neurons in primary somatosensory regions (S1) as the effect's origin (Geldard, 1975, 1985; Geldard & Sherrick, 1972, 1986). Several findings corroborated this view. For instance, the illusory rabbit was reported to not cross the body midline (Geldard, 1982, 1985; but see Eimer et al., 2005; Trojan et al., 2010 for opposing results); the size of the illusion appeared to covary with the receptive field size of the presumed corresponding neurons in S1 (Geldard & Sherrick, 1983); and the only neuroimaging study that has investigated the rabbit phenomenon (Blankenburg et al., 2006) observed similar activity in S1 when a location was truly stimulated and when it was perceived due to the rabbit illusion. In fact, the illusory percept of a location in the middle between the two truly stimulated locations also lay at an intermediate S1 position, suggesting a parallel of the perceived stimulus pattern and neural S1 activity.

If the suggestion were true that the cutaneous rabbit effect is bound to anatomy, the rabbit illusion would be limited to 2D skin space and, in extension, to neighboring neural regions in S1. Accordingly, it could not occur across distant body parts, such as an arm and a leg. Yet, the idea that tactile spatiotemporal illusions are bound to the body, or anatomical space, is at odds with the proposition that they are based on expectations about interactions with the environment: Objects in the environment move in external space. Only under very specific circumstances are anatomical and external space aligned. For example, when sitting on the grass at a picnic, ants will crawl from one finger to the next, and from the hand onto the leg when you're resting your arms on your lap. They will not only walk along single limbs. Hence, they create sensory signals in receptive fields that are remote in anatomical space. Establishing a prior based on neighboring receptive fields (i.e., anatomical space) would not faithfully reflect these experiences. Thus, it is insufficient to take into account only anatomical space to tune the brain to movement in space. Accordingly, such a strategy would not be an optimal adaptation to interacting with the environment.

Some studies have indirectly related the rabbit illusion to external space. For instance, a rabbit percept was found to cross the midline at the abdomen, implying involvement of both hemispheres (Trojan et al., 2010). Stimuli were also perceived as if moving along a stick held between the index fingers while only the fingers had been stimulated, showing that the cutaneous rabbit effect could be experienced outside the body (Miyazaki et al., 2010). Last, it has been observed that stimuli presented on both forearms, that is, limbs represented in S1 of different hemispheres, attract each other (Eimer et al., 2005). However, all these studies applied

the rabbit paradigm to homologous body parts. Accordingly, across-limb rabbit percepts may be related to interhemispheric connectivity between homologous body regions of the two body halves, effectively corroborating the dependence of the rabbit percept on anatomically guided neural organization. Finally, two studies have reported rabbit effects between different fingers of one hand (Trojan et al., 2014; Warren et al., 2010). Yet, the fingers, again, activate neurons in neighboring areas of S1, and so rabbit jumps between fingers may not be considered strong evidence for illusory movement in external space. Overall, then, a growing number of studies have casted doubt on the original proposal that illusory localization, as observed in the rabbit illusion, is solely determined by anatomical criteria, but none of them has provided strong and explicit evidence for a determining role of external space in the priors reflected by the illusion. Here, we present direct evidence for an important role of external spatial coding in the rabbit percept. We presented stimulus sequences known to elicit the rabbit illusion to single limbs as well as across two limbs placed next to each other. Stimuli presented to the different limbs were close together in space, because participants placed their limbs next to each other. Under the assumption that tactile stimuli are evaluated in 3D space, our setup made it plausible that the sequences' tactile events were caused by a common origin. The rabbit effect was evident across the two arms, and across an arm and a leg of the same and of opposite body sides. Participants indeed reported that stimuli were distributed along the hypothetical trajectory between the true stimulus locations, whether the sequence was on one limb or whether it was distributed across two limbs. Moreover, participants sometimes reported displaced stimuli on the incorrect limb, implying that perceptually displacing stimuli in space also affected how these stimuli were assigned to a body part. Together, these findings suggest that the cutaneous rabbit effect involves an external-spatial process that can evoke not only spatial distortions but, in addition, categorical errors about the limb on which a stimulus seems to have occurred.

Results

We aimed to test whether the expectations about movement that underlie spatiotemporal tactile illusions are related to external space. We induced the cutaneous rabbit effect on single limbs and across different configurations of upper and lower limbs as well as within and across body sides. By varying stimulation patterns and limb configurations, we separated the influence of anatomical space, external space, and the role of homologous regions on the two body sides and, accordingly, the potential role of connections between homologous brain regions in the two hemispheres. We then fitted participants' behavior with a Bayesian observer model, originally proposed by Goldreich and Tong (2013), and found that it reproduced key aspects of participants' localization behavior in multi-limb configurations when not anatomical but external-spatial priors are used.

Experiment 1

Nineteen participants received sequences of brief vibrotactile stimuli and reported where they had felt each stimulus by clicking on a picture of the respective limb(s) on a computer screen using a trackpad. We used the following limb configurations: (single) arm (A), (single) leg (L),

two arms (AA), arm and leg of the same body side (Arm Leg - one side, AL-1s), and arm and leg of different body sides (Arm Leg - two sides, AL-2s). Each limb configuration was tested with two tasks. In the first task, participants localized single stimuli to yield an estimate of general localization performance as a baseline (Trojan et al., 2010). In the second task, they localized three consecutive tactile stimuli in perceived order (see Figure 1 for a detailed description of stimulus locations and sequences). In one-limb configurations (A, L), all three stimuli occurred on the respective limb. In two-limb configurations (AA, AL-1s, AL-2s), the three stimuli could all three be presented on one of the two limbs, or distributed across both limbs. Presenting the three stimuli on one limb allows us to ascertain that the illusion occurred even if other limbs are task-relevant. This is not the case in traditional setups with stimulus sequences on a single arm and, thus, served to ascertain that the illusion occurs normally in our extended setup; we report these single limb results in Supplementary File 1. Here, our focus was on trials in which the three stimuli were distributed across the two involved limbs, with the first two stimuli presented on the first limb, and the final stimulus on the second limb.

Independent of whether one or two limbs were stimulated in a given sequence, we used three different types of stimulus sequences (see Figure 1). In all of them, the Euclidian distance between the first and third stimuli was always 10 cm, and the three sequence types differed only with respect to the second stimulus.

The first sequence type were illusory rabbit sequences that aimed to elicit the rabbit illusion. Here, the second stimulus occurred in the same location as the first, with stimulus onset asynchronies (SOA) of 700 ms between first and second, and 100 ms between the second and third stimuli (Eimer et al., 2005).

The second sequence type were time control sequences. Here, stimuli occurred in the same locations as in the illusory rabbit sequences, but the SOA was 700 ms between all stimuli. These sequences served as controls, as previous work has established that the rabbit percept is strongly reduced (even if not completely obliterated) with this stimulus timing, compared to the fast, 100 ms SOA of the illusory rabbit trials (e.g. Trojan et al., 2010).

The third sequence type were location control sequences. Here, the second stimulus was presented at a location between the first and third stimuli. We included these sequences so that participants would not be biased against reporting the second stimulus at intermediate positions. Thus, they obscured the aim of the experiment and allowed us to check whether participants' responses were coherent.

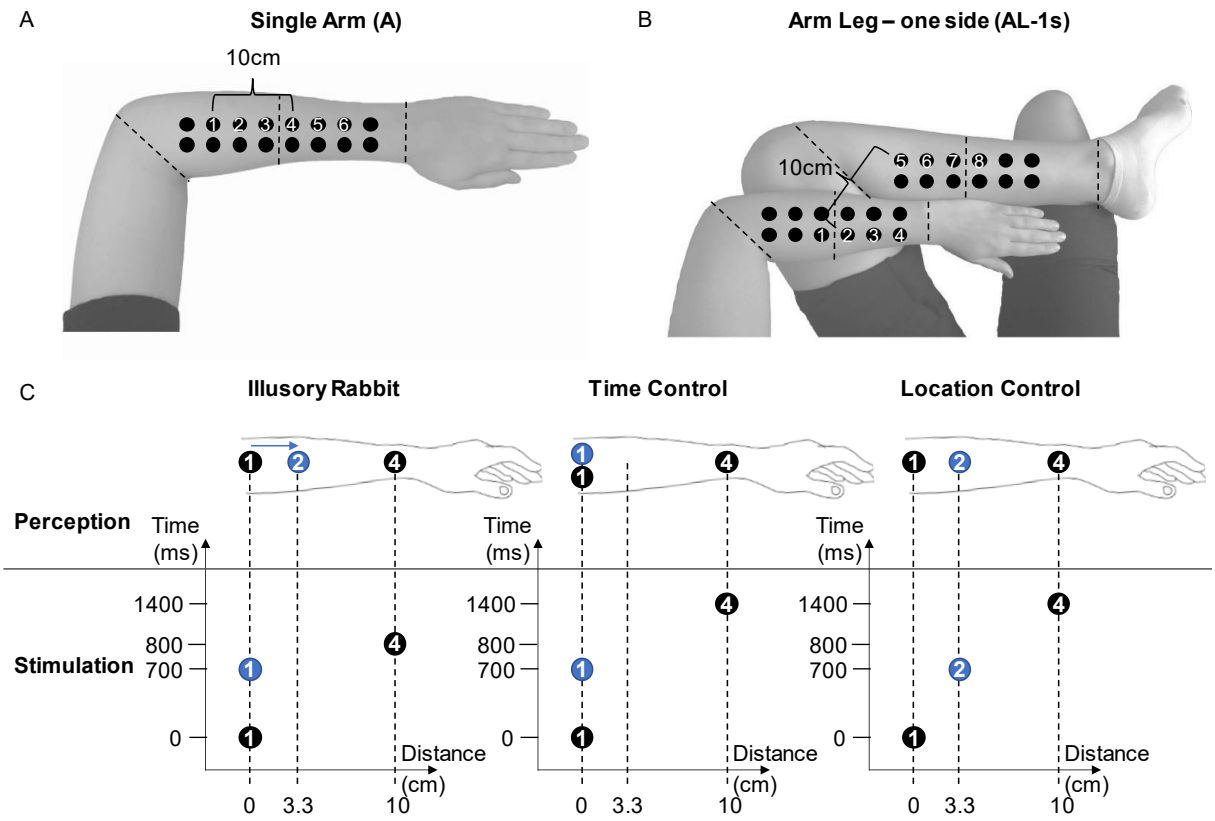

Figure 1. Stimulator positions for A/the single arm (A) and B/the arm leg – one side (AL-1s) configuration when stimulating the left body side. *The positions were similar in the other limb configurations. We used only the 8 numbered stimulators; all others were attached only to obscure the relevant locations to participants at all times. In all configurations, the distance between the first and last stimuli was always 10 cm (e.g. stimulus positions 1-1-4 or 7-7-4). The dashed lines represent the landmarks used to place the stimulators (distance elbow/wrist or knee/ankle and their midpoint, see Methods).* ***(C) Schematics of the three-stimulus sequences*** (Goldreich, 2007)***.*** *Each panel schematically depicts one sequence. Numbered circles represent the three stimuli, with the numbers indicating the temporal order of the sequence (and matching the true number of the stimulator in panels A and B). In illusory rabbit and time control trials, the first and second stimuli occurred on the same skin location (same vertical dashed line). In the location control trials, the second stimulus was in a different location between the first and last stimulus (3.3 cm from the first stimulus in the example of the depicted 1-2-4 sequence); in two-limb configurations, the second stimulus could be on the same limb (e.g. 2-3-5 in panel B) or not (e.g. 4-6-7 in panel B). The first and third stimuli were always 10 cm apart. The Stimulus Onset Asynchrony (SOA) between the first and second stimuli was always 700 ms. The SOA between the second and third stimuli was either 100 ms or 700 ms, depending on stimulus sequence, as indicated on the y-axis. The resulting perception is indicated on the schematic drawing of the arm above the axis grids: in the illusory rabbit, the perception of the second stimulus is often shifted towards the third (as indicated by the blue arrow). In the two other sequences, the second stimulus is usually perceived near its true location. .*

Correct localization of single stimuli

In the first task, we presented only a single stimulus in a given trial. Participants localized stimuli on the correct limb in 98.6% (AA), 99.3% (AL-1s) and 98.9% (AL-2s) of the two-limb configuration trials. For all one and two-limb configurations, reported single stimulus locations differed significantly between the different stimulated skin locations (all $p < .001$, see Table S1 in Supplementary File 1), indicating that participants were able to discriminate between the different stimulated positions.

Higher proportion of illusory displacements in illusion than control trials

Now, having confirmed that participants were well able to localize the stimuli as such, we analyzed localization in the second task that involved the three-stimulus sequences. We introduced stimulus patterns known to elicit the rabbit percept, which is defined as perceiving the second stimulus as displaced towards the location of the third stimulus. We investigated how frequently a rabbit percept was reported and whether this effect was modulated when stimulation spanned two limbs; in two-limb configurations, our analyses focused on stimulation sequences with stimulation of both limbs. We analyzed whether localization of the middle stimulus differed between the three-stimulus sequences (illusory rabbit, time control, and location control sequences; Figure 1). We first calculated the Euclidean distance between the reported locations of the first and third stimuli and projected the reported second stimulus location onto this line (Trojan et al., 2010, 2014, 2019). Data inspection revealed that the distribution was not normal, but rather comprised a large proportion of values near 0 (see Figure S1 in Supplementary File 1), indicating a proportion of trials in which the second stimulus had been veridically perceived near its true location identical to that of the first stimulus (i.e., an illusion was not elicited; see Figure 1); absence of the illusion was more frequent in control sequences, a result that validates the experimental design. To model the bimodal distribution of reported locations, we used a two-part modelling approach (Sauzet et al., 2019). With this analysis strategy, response data were first dichotomized based on whether the illusion was present (i.e., second stimulus displacement > 10%) or not (i.e., second stimulus displacement < 10%; this cut-off value is arbitrary; other cut-off values, e.g., 5%, render comparable results, see Table S3 and Figure S2 in Supplementary File 1). Statistical modelling investigated the frequency of the rabbit percept per *Limb Configuration* (A, L, AA, AL-1s and AL-2s) and *Stimulus sequence* (illusory rabbit vs. time control or illusory rabbit vs. location control). In a second step, the magnitude of the displacement was analyzed only for the subset of trials that were classified as having elicited the rabbit illusion. Statistical analysis involved the same factors as the first analysis. We performed separate analyses to compare illusory rabbit sequences to the different types of control sequences, because each type of control sequences involved a specific spatial pattern for the three-stimulus sequence (see Figure 1), so that three sequence types could not be meaningfully compared within a single analysis.

In illusory rabbit sequences, 75.9% of participants' second stimulus localizations were classified as indicating a rabbit percept. Mislocalization was also evident in time control sequences, but at a lower proportion of 45.5%. Stimulus displacement in time control sequences in a large proportion of trials, as seen here, is a regular finding (Asai & Kanayama, 2012; Warren et al., 2010), with a small displacement even at SOA of >1000 ms between the second and third stimulus (Trojan et al., 2010). Importantly, the difference in proportions between sequences was significant (generalized linear mixed model's – GLMM – fixed main effect of factor *Stimulus Sequence*, $\chi^2(1) = 39.61$; $p < .001$), indicating a higher occurrence of illusory displacement in illusory rabbit trials. There was also a significant main effect of *Limb Configuration* ($\chi^2(4) = 93.7$; $p < .001$) and an interaction between the two factors ($\chi^2(4) = 35.23$; $p < .001$). Nevertheless, post-hoc comparisons indicated that the probability to report a displaced second stimulus location was higher in illusory rabbit than in time control sequences for all limb configurations (all $p < .001$; see Figure 2 and Table 1). Moreover, the illusion

occurred more often when all stimuli were presented on a single arm than in all other limb configurations ($p < .021$ for all post-hoc comparisons with the single arm configuration; see the bigger difference between the means of the blue and red violins for this configuration in Figure 2). The remaining limb configurations did not differ from each other, suggesting that the proportion of reporting a displaced second stimulus was comparable across these limb configurations (all $p > .327$).

In sum, participants reported a displaced second stimulus, indicative of having perceived the rabbit illusion, in all the limb configurations. Thus, the rabbit illusion occurs across two homologous limbs (AA) as well as across different types of limbs (AL-1s and AL-2s) and even across the body midline (AL-2s).

Table 1. Post-hoc comparisons of the frequency of rabbit percept, for each stimulus sequence, in time control vs. illusory rabbit stimulus sequences. *P values are FDR-corrected.*

stimulus sequence	limb configuration	odds ratio	SE	df	z ratio	p value
Time control vs. Illusory Rabbit	Arm (A)	0.044	0.01	Inf	-10.42	<0.001
	Leg (L)	0.135	0.04	Inf	-6.86	<0.001
	Two arms (AA)	0.203	0.06	Inf	-5.80	<0.001
	Arm Leg - one side (AL-1s)	0.177	0.05	Inf	-6.11	<0.001
	Arm Leg - two sides (AL-2s)	0.171	0.05	Inf	-6.29	<0.001

Not surprisingly, in location control sequences (three different stimulus locations; yellow violins in Figure 2), participants usually reported the second stimulus at a different location than the first – recall, that in these trials, the second stimulus was truly presented at an intermediate position. For comparability, we employed the same criteria to classify a difference in localization between two stimuli here as in the illusory rabbit sequences; in other words, we classified two stimuli to have been reported as spatially different if their locations differed more than 10% of the total reported sequence distance. Any deviation from 100% in this control condition, in which the stimuli were truly presented at different locations, can serve as an indicator for the upper bound of a reported displacement >10% in any other condition, for instance due to variability in indicating positions on the picture on the screen etc. With this criterion, the second stimulus was reported at a different location than the first in 80.9% of trials. This proportion is slightly, but significantly higher than in illusory rabbit sequences, as shown by a main effect of *Stimulus Sequence* ($\chi^2(1) = 4.31$; $p = .038$). There was no evidence for a modulation by the involved limbs, with neither a main effect of *Limb Configuration* ($\chi^2(4) = 1.88$; $p = .758$) nor an interaction between *Stimulus Sequence* and *Limb Configuration* ($\chi^2(4) = 7.31$; $p = .121$). Thus, although participants reported an illusory displacement in a large number of trials, the illusion did not occur in all illusory rabbit trials. However, the illusory rabbit sequences differed much less from location control sequences (on average, -5%) than from time control sequences (+30%), suggesting that the illusion arises quite reliably.

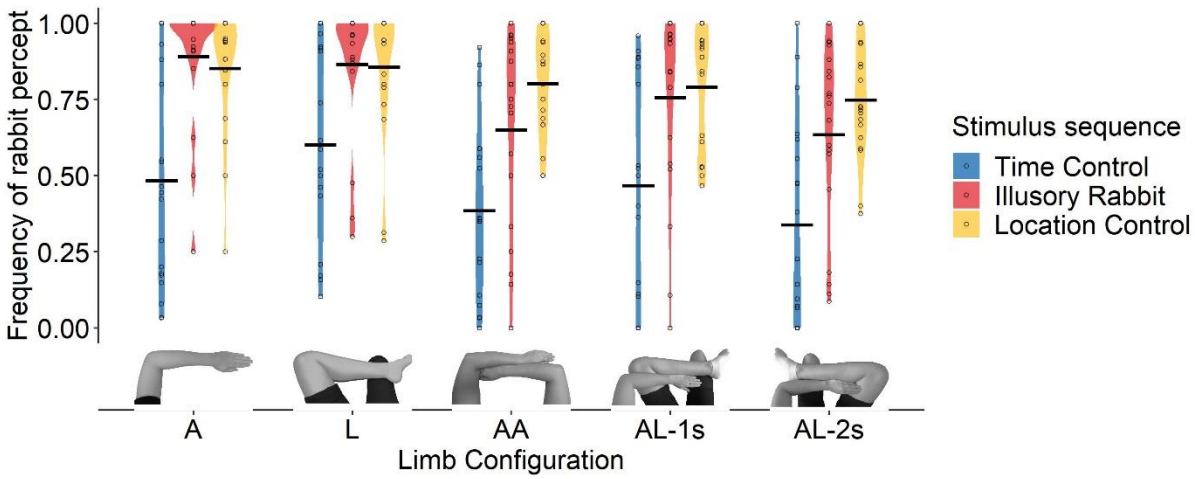

Figure 2. Frequency of the rabbit percept per Limb configuration and Stimulus Sequence.*; Horizontal black line represents the mean frequency of reporting second stimulus as displaced from the first, and violins the distribution across all stimulus sequences of a given sequence type. Black dots represent the mean frequency of reporting a displaced second stimulus for single participants. A = Single Arm; L = Single Leg; AA = Two arms; AL-1s = Arm Leg - one side; AL-2s = Arm Leg - two sides.*

Larger displacement in illusion than in control trials

Our previous analysis implies that illusory displacements were also elicited in trials designed as non-illusion control trials. Although this is not an unusual result (Asai & Kanayama, 2012; Trojan et al., 2010; Warren et al., 2010), we next asked whether the size of the illusory displacement was comparable in the different trial types. We restricted our analysis to trials in which a >10% displacement had been reported. Thus, displacement could range from a small, 10%, to a full, 100% displacement. The displacement was 51.8% in illusory rabbit stimulus sequences, but only 35.0% in time control stimulus sequences, indicating smaller illusory displacement in control than in illusion sequences. The difference was significant, evident in a main effect of *Stimulus Sequence* ($\chi^2(1) = 35.2$; $p < .001$). Although there were a main effect of *Limb Configuration* ($\chi^2(4) = 11.6$; $p = .021$) and an interaction between the two factors ($\chi^2(4) = 14.0$; $p = .007$), post-hoc comparisons confirmed the effect of stimulus sequence for all limb configurations (all $p < .001$; see Figure 3 and Table 2).-The displacement was smaller in the AA than in the AL-1s configuration (SE = 2.54, $t = 3.26$, $p = .018$) and the L configuration (SE = 2.32, $t = 3.04$, $p = .021$; see Figure 3). No other comparisons between limb configurations were significant (all $p > .074$).
In summary, these results indicate a larger displacement in illusory rabbit than in time control trials, both for single-limb and for two-limb configurations and irrespective of whether limbs belonged to the same body side or not.

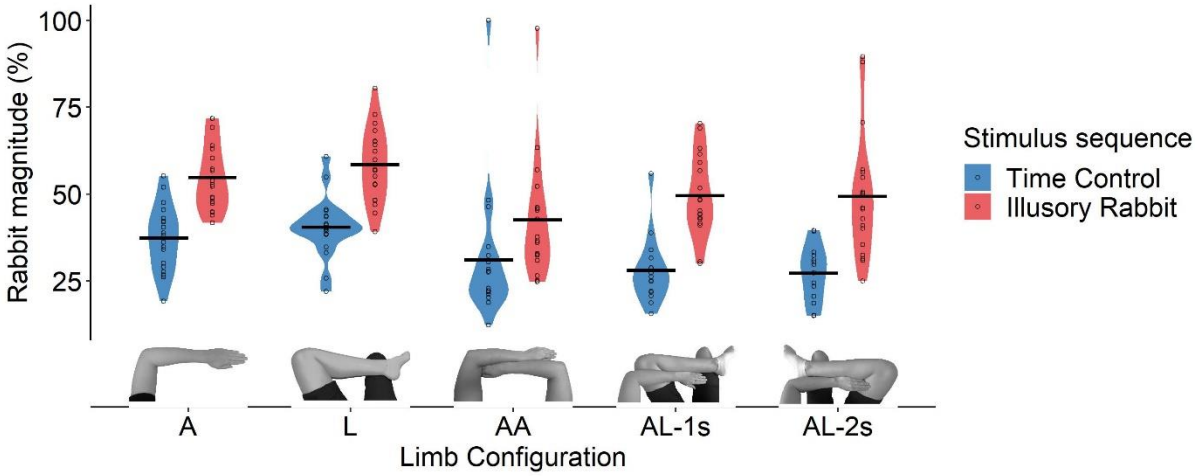

Figure 3. Displacement of the second stimulus, indicative of illusion strength, per Limb configuration and Stimulus sequence. *Horizontal black line represents the mean displacement of the second stimulus, and violins the distribution across all stimulus sequences of a given sequence type. Black dots represent the mean displacement for single participants. A = Single Arm; L = Single Leg; AA = Two arms; AL-1s = Arm Leg - one side; AL-2s = Arm Leg - two sides. Data for the location control trials is not shown as it would be an average of truly stimulated positions, and it would not be informative to compare it to the illusory rabbit trials.*

Table 2. Post-hoc comparisons of the degree of displacement, for each configuration, in time control and illusory rabbit sequences. *Estimate indicates the differences in percent of displacement.*

stimulus sequence	limb configuration	estimate	SE	df	t ratio	p value
Time control vs. Illusory Rabbit	Arm (A)	-17.2	1.92	40.96	-8.94	<0.001
	Leg (L)	-18.7	1.87	37.74	-10.01	<0.001
	Two arms (AA)	-11.6	2.24	76.36	-5.18	<0.001
	Arm Leg – one side (AL-1s)	-19.9	2.16	62.51	-9.20	<0.001
	Arm Leg – two sides (AL-2s)	-14.5	2.44	104.0	-5.94	<0.001

The rabbit jumps from limb to limb

So far, we have shown that the rabbit illusion is comparable when it involves homologous and non-homologous limbs, suggesting that it is not bound to skin space, but can arise in external space. The stimulus sequence for the illusion always presents the first two stimuli on one limb, and only the third stimulus on the other limb (e.g., Figure 1B, stimulus patterns 2-2-5, 6-6-3 etc.). Our sequences were arranged such that the distance between the first and third stimulus covered both involved limbs to an approximately equal amount. Therefore, if the illusion were based on interpolating a trajectory in 3D space, then the second stimulus should be perceived on the second limb when it was reported to be displaced by more than 50% towards the last stimulus; that is, in such cases, the second stimulus would have been applied to one, but perceived on the other limb due to the rabbit-like interpolation of hops along the trajectory between the outer stimuli. As shown above, participants reported a large range of illusory locations for the second stimulus, so that assignment to the second limb should occur in some, but not all trials.

We assessed how often participants reported the second stimulus on the wrong limb in two-limb configurations. As previously, we restricted this analysis to trials in which a rabbit percept

had occurred according to our 10% displacement criterion, and to sequences that stimulated both involved limbs (rather than just presenting all three stimuli to one of the two involved limbs). Participants reported the second stimulus on the wrong limb in 36.8% of illusory rabbit sequences. In contrast, this judgment error occurred in only 6.2% of time control sequences (main effect of *Stimulus Sequence* ($\chi^2(1) = 24.88$; $p < .001$). The main effect of *Limb Configuration* ($\chi^2(2) = .423$; $p = .81$) and the interaction between the two factors ($\chi^2(2) = 4.94$; $p = .084$; see Figure 4) were not significant. Thus, participants attributed the second stimulus to the incorrect limb particularly in illusory rabbit sequences across all limb configurations.

In our second type of control sequence, the location control sequences, stimuli occurred at three distinct locations. Here, the second stimulus occurred on the first limb in some, and on the second limb in other trials. Participants usually reported the correct limb (mean error: 5.3%), significantly different from the proportion of errors in illusory rabbit sequences (main effect of *Stimulus Sequence* ($\chi^2(1) = 19.6$; $p < .001$; see Figure 4). Again, there was no evidence for differences between limb combinations (main effect of *Limb Configuration* ($\chi^2(2) = 1.84$; $p = .40$; interaction of *Stimulus sequence* × *Limb Configuration*, $\chi^2(2) = 3.29$; $p = .19$; see Figure 4). Note, that errors were comparable in the two types of control sequences, and, thus, that frequent attribution to an incorrect limb was, therefore, a phenomenon unique to illusory rabbit sequences.

In sum, these results suggest that the second tactile stimulus perceptually jumped to the other limb in about one third of those trials in which the rabbit illusion was elicited. Incorrect assignment occurred in all two-limb configurations alike, including configurations that involved an arm and a leg. In other words, when the trial involved an arm and a leg, the middle stimulus was frequently mislocalized from an arm to a leg, or vice versa.

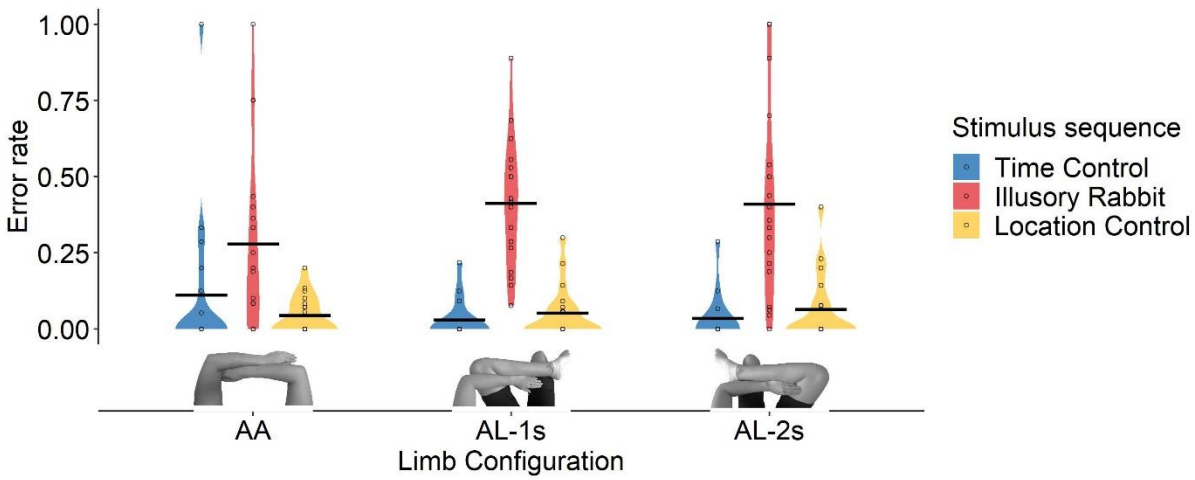

Figure 4. Error rate per Limb Configuration and Stimulus Sequence. *Horizontal black line represents the mean error rate, and violins the distribution across all stimulus sequences of a given sequence type. Black dots represent the mean error rate for single participants. AA = Two arms; AL-1s = Arm Leg - one side; AL-2s = Arm Leg – two sides.*

This finding entails that the rabbit's hops are not just distributed along the skin, but that the rabbit can hop to a distant and non-homologous body part, presumably because the tactile stimulation pattern implies a movement in space towards the second limb. Thus, it suggests that the influence of expectation on perception is so strong that even the limb where touch is felt is "corrected", a remarkable effect that defies explanations of the rabbit effect in terms of

interactions between peripheral receptive fields or S1 neighboring neurons. Notably, previous studies have observed such jumps between body parts only between fingers of a same hand (Trojan et al., 2014; Warren et al., 2010), that is, skin regions that are represented in neighboring areas of primary somatosensory cortex of one hemisphere.

However, some alternative explanations need to be ruled out. One consideration is that, in our setup, participants indicated the felt location of the three tactile stimuli on a trackpad, based on a photograph that displayed their current limb configuration. It is possible that participants did not always respond with high accuracy. In particular, participants may have attempted to indicate the border region of the first limb, but accidentally indicated a region on the picture that already belonged to the other limb. However, visual inspection of the distribution of reported locations on the photographs did not suggest that this was the case: most responses were, in fact, clearly inside one or the other limb (see Figure S3 in the Supplementary File 1).

Another consideration is that the fast stimulation we employed to elicit the rabbit illusion may have increased the level of uncertainty about the stimuli's locations compared to the slower stimulation patterns of the control sequences. Accordingly, participants may have been unsure about where the second stimulus had occurred and, when this occurred, may have chosen a random location on the photographs without actually having had a clear percept of a stimulus on that limb.

We addressed these alternative explanations with a new experiment in which we explicitly assessed on which limb the second stimulus had been perceived and how confident participants were about their judgments.

Experiment 2

Twenty new participants received tactile three-stimulus sequences with the same spatial locations and timings as in Experiment 1, that is, illusory rabbit, time control, and location control sequences (see Figure 1). We restricted the experiment to stimulation of the left arm and leg, as this configuration had shown the highest proportion of reported stimulus displacement and stimulus assignment to the incorrect, second limb in Experiment 1. For each stimulus sequence, participants indicated by a button press on which limb they had felt two of the three stimuli. For some trials, participants additionally rated their perceptual confidence. If the response was correct, a confidence rating was presented with a probability of 20%. If the response was incorrect, confidence was assessed with a probability of 80%. Participants were not informed about whether their responses were correct or not and were unaware of our sampling strategy. Confidence ratings had two parts: participants first indicated whether they thought they had pressed the correct button (yes/no), and then rated their confidence about this judgment on a numerical rating scale from 0% to 100% certainty, implemented as a mouse-controlled slider on the computer screen.

Participants' choice about which limb received two stimuli indicates whether they assigned the second stimulus to a wrong limb. The first stimulus was always presented on the first limb, and the third stimulus on the second limb, and these stimuli had not been subject to substantial perceptual displacement in Experiment 1 (see also *Bayesian Modelling* section). In both illusory rabbit and time control sequences, the stimulus sequence always began with two identical stimuli. Hence, if a participant reported to have felt two stimuli on the *second* limb, this response implies an incorrect assignment, that is, a jump across limbs, of the second stimulus.

Illusory jumps to the other limb occur irrespective of response mode

Participants reported to have perceived two stimuli on the second limb, indicative of the illusory rabbit stimulus having been assigned to the incorrect limb, in 12.3% of the trials in illusory rabbit sequences, but only in 5.1% of time control sequences ($\chi^2(1) = 37.2$; $p < .001$; Figure 5), and 6.8% in location control sequences ($\chi^2(1) = 9.5$; $p = .002$; Figure 5).
Thus, Experiment 2 corroborates our finding from Experiment 1 that incorrect assignment can occur between arms and legs. Errors were less frequent in Experiment 2 (compare Figure 4 and Figure 5). When based on the total number of trials, they occurred 31.8% of Experiment 1's illusory rabbit trials. This difference in numbers is likely due to methodological factors. First, Experiment 1 involved presenting participants with a photograph of their limb configuration; this visual information may have influenced the spatial judgments made by participants. Second, Experiment 2 posed only a single binary question directly following stimulation; in contrast, Experiment 1 required reporting all three stimuli, and the prolonged occupation with stimulus localization may have influenced participants' responses. Importantly, the lower frequency of errors across limbs does not mean that the rabbit illusion occurred less frequently in Experiment 2, given that our measure was designed to specifically assess incorrect assignment across limbs but is agnostic about any illusory displacement that occurred when the second stimulus was correctly perceived on the first limb.

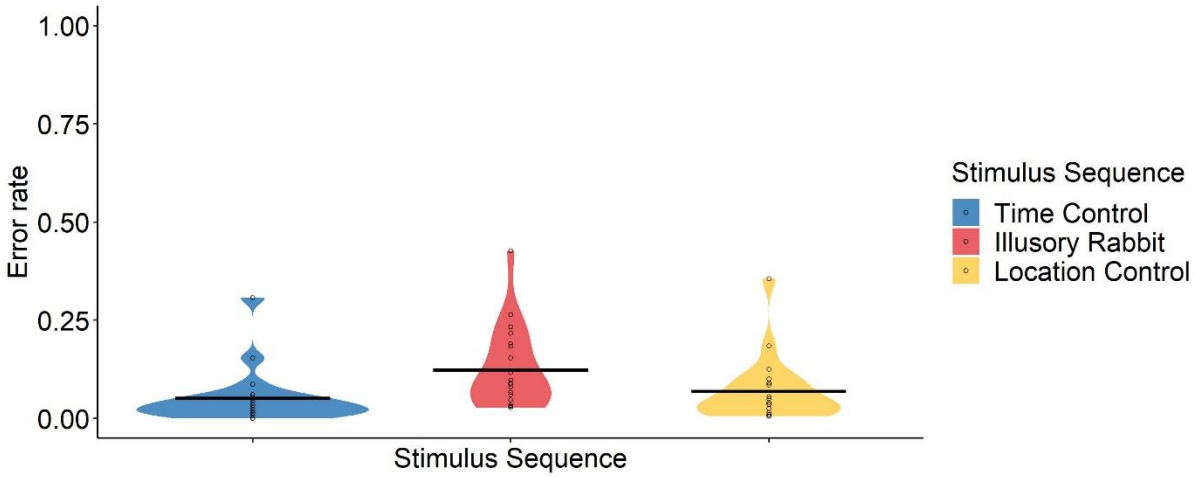

Figure 5. Error rate per Stimulus Sequence. *Violins represent the distribution across all the stimulus sequences. Horizontal black line represents the mean. Black dots represent mean error for single participants.*

Rabbit jumps are not a result of perceptual uncertainty

Having confirmed that participants had perceived wrongly assigned stimuli from one to the other limb in Experiment 2, we next turned to the question whether such reports may have simply resulted from confusion and uncertainty evoked by the unusual stimulation pattern. To this end, we compared reported confidence about the responses across sequences. We excluded trials in which participants stated that they had responded incorrectly (5.2% of ratings). Given that we obtained ratings in ~80% of trials with an incorrect response without participants being aware of an incorrect answer, our data contained many trials in which participants reported a stimulus on the wrong limb but were obviously unaware of their error.

As before, we compared rabbit illusion sequences separately to time control and location control sequences. Both LMMs revealed a significant interaction between *Accuracy* (correct/incorrect) and *Stimulus Sequence* (illusory rabbit vs. time control: $\chi^2(1) = 12.7$; $p < .001$; illusory rabbit vs. location control: $\chi^2(1) = 4.60$; $p = .032$). Confidence was comparable across the different stimulus sequence types when participants gave incorrect responses (illusory rabbit sequences: 66.7%; time control sequences: 69.3%; location control sequences: 72.9%; all post-hoc comparisons are detailed in Supplementary File 2; see Figure 6). Recall that errors in illusory rabbit trials indicated that the second stimulus was perceived on the wrong limb; thus, there is no evidence that such mislocalization was accompanied by a reduction in confidence compared to any other stimulus sequence.

As is common, confidence was higher for correct than for incorrect responses (e.g. Badde et al., 2019; Fleming & Frith, 2014), indicated by significant main effects of *Accuracy* ($\chi^2(1) = 63.8$; $p < .001$ and $\chi^2(1) = 52.0$; $p < .001$ for illusory rabbit vs. time control and location control respectively). However, when participants gave a correct response, their confidence was lower in illusory rabbit than in time control sequences (84.8% vs. 92.8%; $t(21) = 5.8$, $p < .001$) and location control sequences (84.8% vs. 91.7% respectively; $t(23) = -4.2$, $p < .001$; see Figure 6). Given that the number of incorrect responses differed across sequence types, but confidence was comparable for incorrect responses of all sequences, this suggests that uncertainty is unlikely to have played a role in the emergence of the rabbit illusion percept. Yet, we further tested whether uncertainty fully explains sequence differences in our experiment by adding confidence ratings as a covariate in a GLMM. If errors were merely a by-product of uncertainty, then any differences between illusory rabbit and time control sequences should be eliminated once variance induced by confidence ratings is accounted for. To the contrary, the main effect of *Stimulus Sequence* was significant also when *Confidence Rating* was included as covariate ($\chi^2(1) = 30.1$; $p < .001$).

In sum, differences in perceptual reports across stimulus sequences were not explained by differences in confidence. Thus, incorrect assignment of the second stimulus from one limb to another in the context of the rabbit illusion was not caused by perceptual uncertainty.

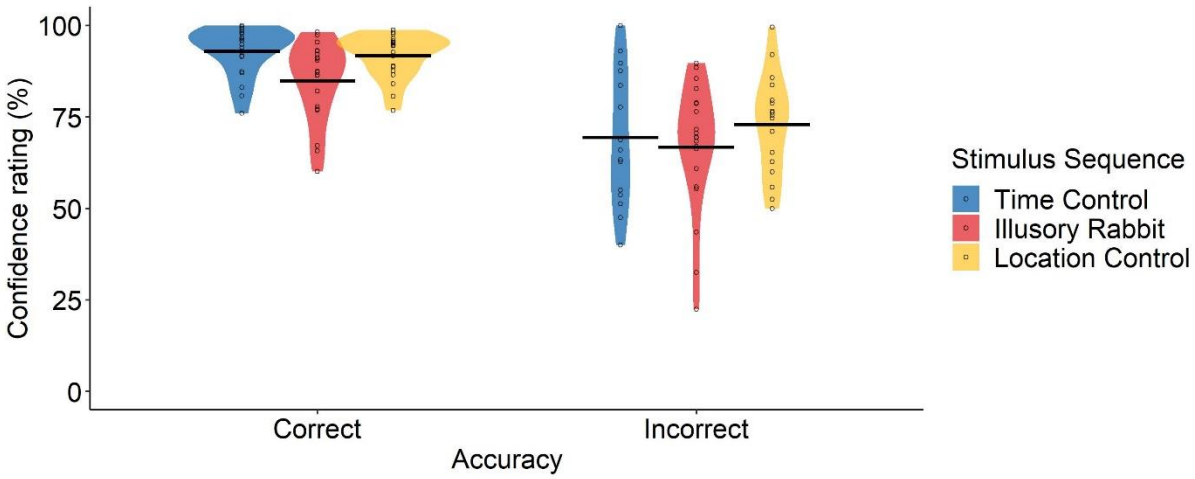

Figure 6. Confidence ratings in Experiment 2 for the different stimulus sequences, when participants were correct vs. incorrect. *Incorrect response in time control and illusory rabbit sequences imply that the second stimulus was perceived on the wrong limb. Violins represent the distribution across all the stimulus sequences. Horizontal black line represents the mean. Black dots represent mean error for single participants.*

Bayesian observer model

We observed a rabbit effect between two limbs, suggesting that the cutaneous rabbit illusion is based on external, not only anatomical space. But is this a sign of a statistically optimal integration as suggested by Bayesian accounts of perception? A Bayesian observer model (Goldreich, 2007; Goldreich & Tong, 2013) has been proposed as a framework for the cutaneous rabbit effect but has so far only been applied to single-limb scenarios where anatomical and external space are congruent. Many events involve straight or near-straight motion in space; accordingly, we expect that the brain's priors should optimally be tuned to near-straight motion trajectories in external space. This view implies that the Bayesian observer model should capture participants' behavior when we consider the Euclidian distance between the locations of our stimulus sequences. In particular, distance on the skin is large for all two-limb configurations of our experiments, whereas the Euclidian distance was comparable across all configurations. Therefore, we expect the Bayesian observer model to accurately account for the rabbit effect in all limb conditions when we feed it with external-spatial, that is, Euclidian, distance. On the one hand, this outcome would support that space and velocity, as conceptualized in the Bayesian model, are externally based. On the other hand, it would indicate that spatiotemporal integration based on priors is a feature grounded in 3D interaction space and, thus, is not restricted to anatomical space or processing within a single hemisphere. The model predicts where participants perceive each stimulus from a sequence of tactile stimuli based on statistical optimal integration of sensory input with a "low velocity prior". This prior expresses the brain's experience-based prediction that tactile stimuli which follow each other close in time are usually close together in space and regularly originate from one common event or object that moves comparably slowly. For stimuli that imply fast motion, as in the cutaneous rabbit paradigm, the prior shapes perception in a way that stimuli are perceived as closer to each other than they really were, resulting in the observed shift of the second stimulus towards the third. However, the influence of the prior depends on the spatial precision of the stimulus: when precision is low – that is, when the true stimulus's position of the current sensory input is uncertain – then prior experience will be given more weight, effectively "correcting" sensory input towards what is deemed plausible based on experience.

Lower precision for tactile localization on the leg than on the arm

Previous research has shown that tactile precision strongly varies between different body parts and is lower on the leg than on the arm (Mancini et al., 2014; Weinstein, 1968). In our limb configurations of Experiment 1, the Bayesian observer model would therefore predict a stronger rabbit effect on the leg than on the arm. Moreover, for the arm-leg limb configurations it would predict that the rabbit effect depends on direction. It should be stronger when the first two stimuli are presented on the leg, where precision is lower, compared to when they are presented on the arm, where precision is higher. With respect to apparent motion speed, the differences in participants' reports evoked by our illusory rabbit vs. time control sequences illustrate that the rabbit effect depends on stimulus timing: stimulus timing is faster in illusory rabbit than in time control sequences, so that the Bayesian model predicts greater rabbit effects in the former, consistent with our findings.

We computed precision for localization on the different limbs involved in our Experiment 1 and then fitted the Bayesian observer model to single-participant data for the different limb configurations and the illusory rabbit and the time control stimulus sequences. The predicted positions can then be compared with participants' behavior.

We computed precision as the variability of localization error for each participant and limb configuration (see the *Methods* for details). Variability was higher, and thus, precision lower, on the leg than on the arm (see Figure 7). This was evident from a significant main effect of *Limb Configuration* when comparing the single arm and leg configurations in an LMM ($\chi^2(1) = 18.7$; $p < .001$). Comparison of AA, AL-1s and AL-2s configurations in a second LMM that included *Limb* and *Limb Configuration* as factors revealed a significant interaction between the two factors ($\chi^2(2) = 88.7$; $p < .001$); post-hoc analyses further showed a limb difference for AL-1s and AL-2s, each with higher variability for the leg. In contrast, no difference was evident between the two arms in AA (see Table S5 in Supplementary File 3 for pairwise comparisons).

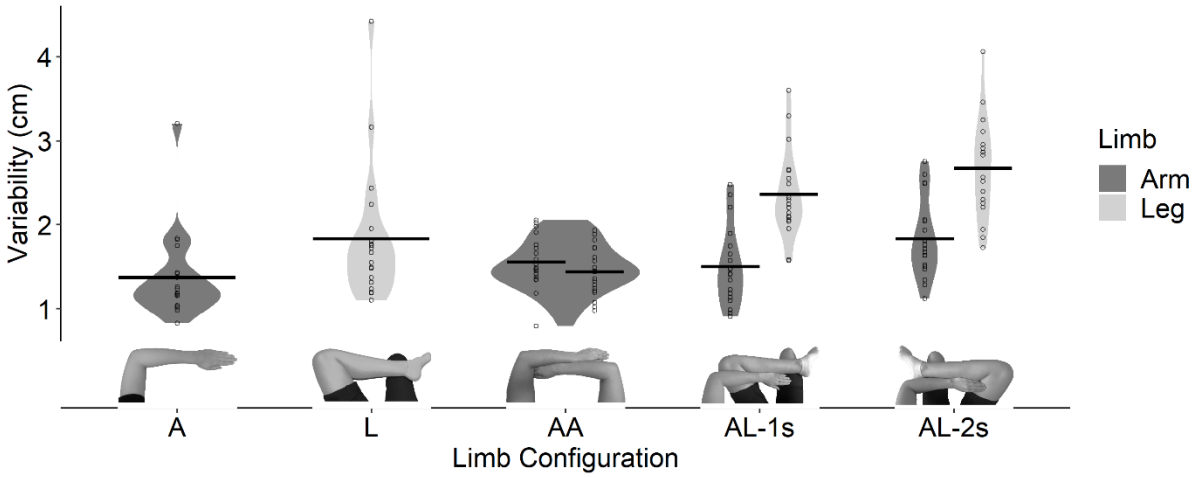

Figure 7. Variability of participants' localization performance for the different limb configurations. *Each point represents the averaged variability (x and y direction combined) for each participant. Lower variability indicates higher precision. Note that values were generally higher on the leg than on the arm, indicating lower tactile precision on the leg. A = Single Arm; L = Single Leg; AA = Two arms; AL-1s = Arm Leg - one side; AL-2s = Arm Leg - two sides.*

Applying the model to three-stimulus sequences

Because the original Bayesian observer model was specified only for pairs of stimuli (Goldreich, 2007; Goldreich & Tong, 2013), we first extended the mathematical formulation so that the model can be applied to the three-stimulus sequences that we used in the present study (see the *Methods* for details). We computed the predicted positions for illusory rabbit and time control stimulus sequences using the respective SOAs as the timing parameters and a low velocity prior of 10 cm/s, as suggested previously (Goldreich, 2007; Goldreich & Tong, 2013). We projected both the predicted locations and the actual (observed) localizations onto a straight line between the positions of the first and third stimulus's centroid. Following these steps, we expressed both predicted and observed localizations for the three-stimulus sequences in a common metric allowing us to directly compare Experiment 1's data with the model's predictions.

The Bayesian observer model made four important predictions that are illustrated in Figure 8A. First, the model predicted that participants should localize the first stimulus in both illusory

rabbit and time control stimulus sequences with high accuracy, which is evident from the predicted locations being close to the zero line that represents the veridical position of the first and second stimuli. This prediction is due to the long SOA of 700 ms between the first and second stimulus; this long time interval diminishes the influence of later stimuli on the first one. Second, for illusory rabbit sequences, the model predicted strong attraction of the second stimulus towards the third stimulus, and also of the third stimulus towards the second stimulus due to the short time interval between them. For time control sequences, however, the model predicted that participants localize the second and the third stimuli close to their veridical positions. Third, the model predicted a slightly stronger displacement of both the second and the third stimuli in the single leg compared to the single arm configuration. This prediction follows from the pattern of lower precision on the leg than on the arm (Figure 7). Fourth, the model predicted direction-dependent illusory displacement for AL-1s and Al-2s, again based on the differences in precision between arms and legs: For AL-1s and Al-2s, the displacements were predicted to be stronger for the second stimulus as well as weaker of the third stimulus for trials with a leg-to-arm than for trials with an arm-to-leg direction.

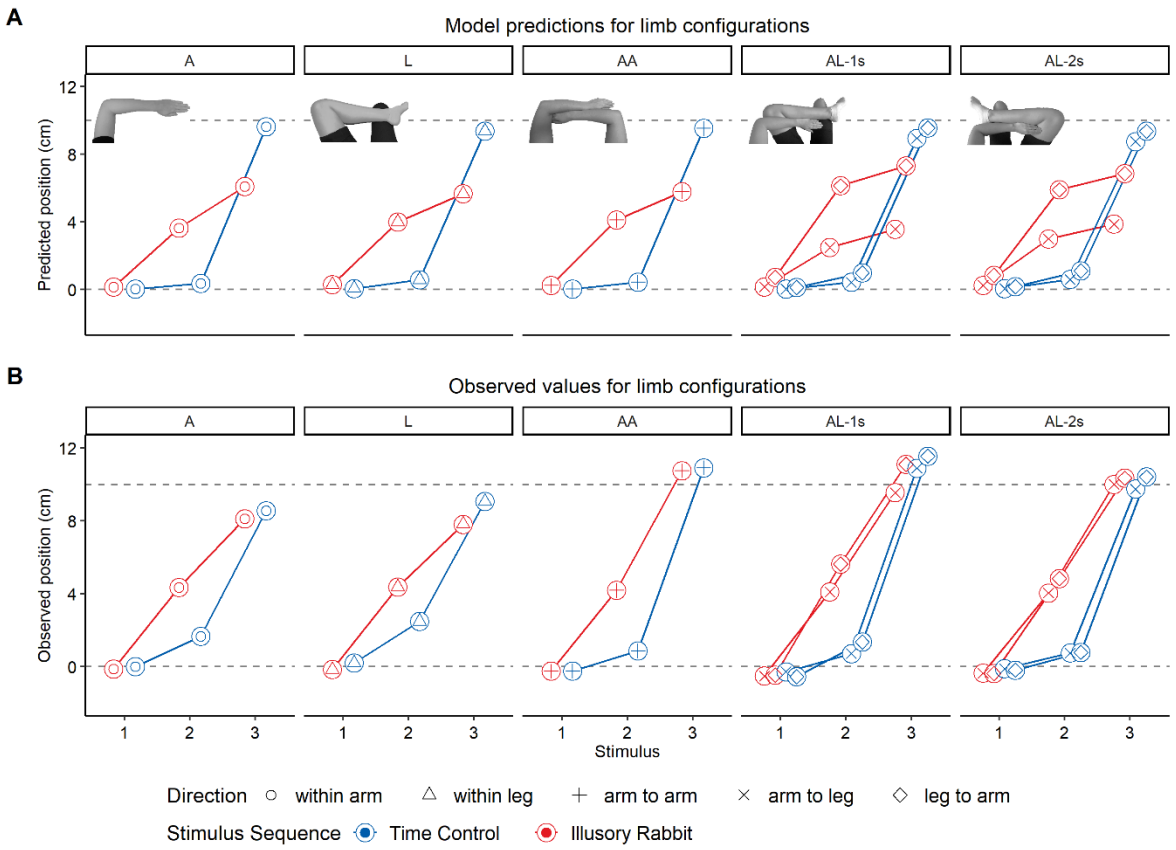

Figure 8. Predicted (A) vs. observed positions (B) for the limb configurations in illusory rabbit and time control sequences. *Positions of the stimuli were predicted using an extended Bayesian observer model based on the model described by Goldreich and Tong (2013). The points represent mean positions (averaged over participants) in cm units along a straight line between the centroids of the respective stimuli. The dashed horizontal line at the y-value of zero represents the veridical position of the first and second stimuli and the dashed line at the y-value of 10 the veridical position of the third stimulus for both stimulus sequences. Illusory displacement is indicated by the second (and in some instances the third) stimuli falling in the area between the two dashed lines. A = Single Arm; L = Single Leg; AA = Two arms; AL-1s = Arm Leg - one side; AL-2s = Arm Leg – two sides.*

Similar patterns for predicted and observed displacements

The experimentally observed positions are shown in Figure 8B. The patterns of observed behavior largely resemble those predicted by the model (see Figure 8A). This is most evident from displacement of the second stimulus towards the third stimulus in all limb configurations in the illusory rabbit compared to the time control sequences. Observed behavior did not match the model's prediction of higher perceived displacement for single leg (L) over arm (A) sequences ($\chi^2(1) = 1.87$; $p = .17$). In contrast, the direction-dependent displacement patterns predicted for AL-1s and Al-2s were reflected in the observed behavior: the positions of the second stimulus in the illusory rabbit sequences were higher for the leg-to-arm than for the arm-to-leg direction in both AL-1s and Al-2s (difference = 1.19 cm; $t(27) = 2.5$, $p = .020$). This result suggests that localization precision of each individual limb affects perceptual reports in the two-limb configurations, in line with a proposed process of Bayesian integration across limbs and hemispheres.

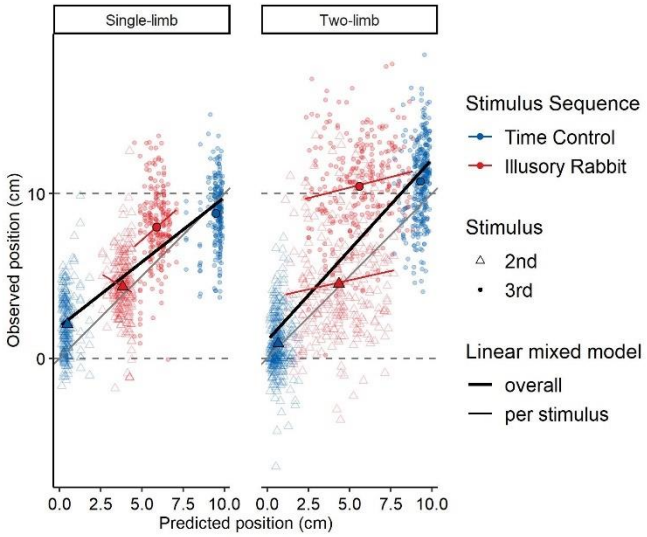

Figure 9. Correlations between positions that were predicted by the Bayesian observer model and observed positions. *The semi-transparent points represent the mean values (averaged over participants) for stimulus patterns separately for the single-limb (Arm and Leg) and the two-limb configurations (Two Arms, Arm Leg - one side, Arm Leg - two sides). For the single-limb, all stimuli were presented within the same limb; in two-limb configurations, all patterns crossed between limbs, for the arm-leg configurations either in arm-to-leg or in leg-to-arm direction. Note that this means that each participant is represented several times in the plot as semi-transparent points; these repeated measurements are accounted for by the linear mixed models used for statistical assessment. The results of the models are shown as the regression lines. The thick black line indicates the regression over the second and third stimuli and both stimulus sequences together; the thin red lines for the illusory rabbit stimulus sequence for the second and the third stimuli separately. The thin grey diagonal line indicates perfect correspondence between model predictions and observed values. Values below this line indicate that positions are over-, values above the diagonal that they are underestimated by the Bayesian model. The larger filled symbols indicate mean values for the stimuli, allowing to see how far the averages diverge from the diagonal line.*

Our model-data comparisons have so far addressed specific hypotheses derived from the Bayesian model; next we evaluated its overall fit to the data when combining all available data in a mixed-effects regression analysis that predicts the observed with the predicted positions. The aim was to evaluate whether there are any differences in model fit between the single-limb configurations, for which the model was originally conceptualized, and the two-limb configurations for which the model has not yet been evaluated. We grouped the AA, AL-1s, and AL-2s limb configurations and compared them against the single limb (A, L) conditions

(analyses for each individual limb configuration are shown in Table S6 in the Supplementary File 3). We restricted the analyses to the second and third stimuli, for which the model made varying predictions depending on the limb configuration and stimulus sequence (see Figure 8) and excluded the first stimulus, for which the predicted positions were invariant. In a first step, we computed an LMM that predicted participants' localization responses from the models estimated localization values across all single- and two-limb configurations. If the model correctly reflected behavior, then plotting observed against predicted localization values would fall onto a unity line of slope 1. The LMM revealed a significant linear relationship between observed and modelled localization responses for both single-limb ($b = .79$, $t(2072) = 28.5$, $p < .001$) and two-limb ($b = 1.1$, $t(2072) = 48.8$, $p < .001$) limb configurations. However, slopes differed significantly between the two ($\chi^2(1) = 78.27$; $p < .001$; see Figure 9). For the single-limb configurations, the slope was < 1, driven largely by the larger-than-predicted displacements of the second stimulus in the time control sequence: participants often reported a displaced second stimulus in the time control sequence (see Experiment 1 and discussion there). This second stimulus displacement in a control sequence also deviates from the predictions of the Bayesian observer model, suggesting that other factors beyond weighted integration play a role in the perception of tactile location. For the two-limb configurations, the slope was > 1, driven largely by the larger-than-predicted location of the third stimulus, especially in the illusory rabbit sequence. This large discrepancy is probably the most obvious mismatch between the Bayesian model and our experimental data. In Figure 9, this mismatch is evident by the third stimulus (red circle) being far above the diagonal line. This location indicates that participants reported the third stimulus closer to its veridical position than the model predicted. An additional LMM revealed that this discrepancy was significant both in the single-limb (difference = 2.1 cm; $t(32.7) = 8.18$, $p < .001$) and the two-limb configurations (difference = 4.9 cm; $t(27.5) = 19.99$, $p < .001$) but significantly larger in the two-limb configurations ($\chi^2(1) = 140$; $p < .001$).

Overall, the model made accurate predictions for both single-limb and two-limb configurations, evident from the near 1:1 relationship of predicted with observed positions in both situations. However, there were systematic discrepancies with respect to a displacement of the third stimulus towards the second stimulus, with the Bayesian model overpredicting displacement. This discrepancy was stronger in the two-limb than in the single-limb configurations.

The previous analysis assessed overall model adequacy across the two stimuli that were affected by our experimental manipulations. Next, we assessed whether differences in sensory precision across participants were consistent with the Bayesian model's prediction separately for the second and the third stimulus. According to the model, the second stimulus should be displaced more towards the third and the third more towards the second the less precise a given participant was able to localize tactile stimuli. If this relationship holds for two-limb configurations, this is evidence that the brain simultaneously considers precisions of different body parts. The LMM indicated that the relationship between predicted and observed locations varied for *Stimulus* (second vs. third stimulus) and *Limbs* (single-limb vs. two-limb configurations; $\chi^2(1) = 5.65$; $p = .017$). The slopes can be compared in Figure 9; they were significantly positive in the single-limb configurations for the third stimulus ($b = .88$, $t(963) = 2.70$, $p = .014$) but not for the second stimulus ($b = -.55$, $t(973) = -1.26$, $p = .207$), and in the two-limb configurations both for the second ($b = .22$, $t(966) = 2.37$, $p = .024$) and the third stimulus ($b = .25$, $t(967) = 2.74$, $p = .014$).

The absence of a significant relationship for the second stimulus in the single-limb configurations may be related to the restricted variance in localization precision in the single-limb configurations (see Figure 9, left panel). Overall, there were mostly positive relationships between individuals' tactile precision and their proneness to the rabbit illusion for each separate stimulus. Yet, regression slopes were clearly below 1, indicating that only a proportion of the variance in the rabbit effect can be accounted for by individuals' sensory precision.

In summary, the magnitude of the rabbit effect is related to participants' perceptual precision even when stimulus sequences include two limbs. This result is in line with the notion of a statistical integration process based on external, Euclidian space. However, there were systematic discrepancies between model predictions and data. First and foremost, the model predicted a stronger displacement of the third stimulus towards the second stimulus than observed, and this discrepancy was especially strong for the two-limb configurations. Perceived displacement of the third stimulus, therefore, appears unique to stimulus sequences along a continuous stretch of and, hence, be an anatomically-based effect. Second, we observed a stronger displacement of the second stimulus in the time control sequences than predicted by the model. It is possible that this effect reflects participants' expectations about stimulus positions based on the statistics of trials presented in the experiment. Participants perceived location control stimuli with veridical displacements of the second stimulus and they might have built up expectations of displacements also for the time control sequences. We conclude that the Bayesian model predicted key features of the localization behavior when using external Euclidian space, but that there are patterns in the data that are not captured by the model. These patterns require additional assumptions about anatomical factors or expectations about locations beyond a simple low-velocity assumption.

Discussion

Humans make large errors when they judge where a touch occurred on their body. In the context of tactile movement, these errors probably stem from reliance on past experience with objects moving across the body surface (Goldreich, 2007; Goldreich & Tong, 2013). Whereas previous accounts of tactile localization bias have focused on early interactions during tactile processing, for instance in the body periphery and in primary somatosensory cortex, we tested here whether tactile localization bias reflects movement trajectories in external space – consistent with the experience available when the body interacts with the world: objects in external space often move along trajectories that touch multiple body parts and do not adhere to the internal organization of the skin.

We addressed this question using the cutaneous rabbit illusion, a reliable tactile mislocalization paradigm that relies on apparent motion. Our study revealed three key findings. First, the cutaneous rabbit effect – a bias to report the second of three tactile stimuli as displaced towards the last stimulus of the sequence – occurred for sequences across two limbs, the two arms or an arm and a leg. In both cases, the stimulated skin regions were anatomically distant. Moreover, the effect was similar when stimuli were presented within and across the body midline, such as when we stimulated an arm and the same-side or opposite-side leg. With respect to distance on the skin, arm and leg locations are almost at a maximal possible distance for the human body. Similarly, arm and leg regions in S1 are distant as well, all the more with limbs across the two body halves. Therefore, the cutaneous rabbit effect did not critically depend on anatomical

proximity of the tactile sequence. Second, the illusory location of the rabbit stimulus – the second stimulus in the sequence of three – was not bound to the limb on which it occurred. Participants frequently reported this stimulus to have occurred on the other limb. Thus, the tactile percept was sometimes wrongly assigned to an anatomically distant body part, even of the other body side. This finding suggests a surprising independence of tactile perception from the original location at which the stimulus touched the skin. Third, critical aspects of participants' localization behavior were reproduced by a Bayesian observer model that integrated all three stimuli of the tactile sequences used in our experiments and used Euclidian distance between tactile locations – independent of which limb the stimulus had been presented to – as input. Thus, mislocalization of apparent motion stimuli is well explained by recurring on external-spatial prior experience. We will discuss these points in turn.

The cutaneous rabbit effect reflects external-spatial priors

External space is the common denominator of all body-world interactions. In other words, if tactile localization errors in the rabbit illusion reflect prior experience with objects and events in the world, mislocalization should reflect typical external-spatial trajectories, that is, straight or near-straight Euclidian trajectories between two tactile locations. Moreover, many such straight-moving objects touch multiple body parts along their way, and therefore the rabbit illusion should not be confined to single limbs. Notably, most previous accounts of the rabbit effect have recurred to local interactions between neurons and their receptive fields in the periphery, or to local neural interactions in primary somatosensory areas (Blankenburg et al., 2006; Geldard, 1975; Geldard & Sherrick, 1983). Nevertheless, an influence of external space on the rabbit effect has been implicit in several previous studies that have demonstrated rabbit effects across arms (Eimer et al., 2005), different fingers of one hand (Trojan et al., 2014; Warren et al., 2010), and on a stick held between fingers (Miyazaki et al., 2010). Here, we demonstrated that the rabbit stimulus was systematically displaced along the Euclidian trajectory between stimuli presented on different limbs and body sides. Our results imply that the localization errors associated with the rabbit illusion are strongly affected by external space and that anatomical units such as a single limb and distance on the skin or in neuronal maps of primary somatosensory cortex do not prevent illusory mislocalization.

It may seem surprising that our results directly contradict Geldard's (1982) original claim that the cutaneous rabbit effect does not cross the body midline. One explanation for these seemingly opposing results is the use of different localization methods. Geldard and collaborators mostly used a sectioning method (Geldard, 1975) in which participants verbally reported the degree of attraction as a proportion of the distance between the anchored outer stimulus positions. In contrast, our and other more recent studies have employed more direct localization methods such as indicating the perceived location by hand pointing (Miyazaki et al., 2010; Trojan et al., 2010) or by localizing the perceived location on a drawing (Flach & Haggard, 2006) or photo (our Experiment 1).

However, a different aspect of previous and our current results may be better able to clear up the seeming contradiction. In our study, the rabbit effect was significantly stronger, with more instances of illusory displacement, when all stimuli were presented on a single limb than when sequences were distributed across limbs. Thus, although involvement of distant skin locations

did not prevent the rabbit illusion, anatomical factors supported its occurrence (Trojan et al., 2014). Thus, both external and anatomical factors appear to shape localization in touch. The idea that anatomical and external space interact has been proposed as the origin of several tactile illusions and effects (e.g. Aristotle Illusion: Hayward, 2008; crossing effect: Badde & Heed, 2016; Heed et al., 2012, 2015; Heed & Azañón, 2014). The influence of anatomical factors is compatible with views that attribute the rabbit effect to early unimodal somatosensory processing (Flach & Haggard, 2006; Geldard, 1985; Geldard & Sherrick, 1972). The multiple spatial influences evident in the rabbit effect, then, likely reflect the organization of the different involved systems – a 2D skin sheet on which touch is first sensed, and a 3D space in which interactions of the own body and other entities take place – and the requirement of interpreting between them to successfully master sensorimotor control (Medina & Coslett, 2010; Tamè et al., 2019).

Assignment of touch to distant limbs

In a significant proportion of trials, participants reported the rabbit stimulus on the wrong limb. To be clear, this result implies that participants perceived stimuli, say, on the leg although they had actually been presented to the arm. We have observed this surprising finding in our two experiments, on two different samples, with two distinct methods. This incorrect assignment could not be explained by uncertainty associated with errors or the context of a perceptual illusion, because modelling confidence along with reported choices did not eliminate the higher proportion of incorrect limb assignments in rabbit as opposed to control sequences. These findings suggest that participants truly perceived tactile stimuli at distant limbs and that this perceptual assignment of stimuli to a limb was influenced by the external-spatial layout of the limbs in our experiment. In a previous report, rabbit effects included incorrect assignment of stimuli between fingers of a same hand (Trojan et al., 2014; Warren et al., 2010). However, we are first to report such incorrect assignment between non-homologous limbs (arm and leg), between limbs of the two body sides, and between body parts that are not neighbors in S1.

A previous study, like ours, presented tactile stimuli along the two arms but concluded that participants did not make errors in assigning stimuli to their true limb (Eimer et al., 2005). However, this conclusion was based on indirect assessment: participants judged whether the second stimulus was perceived at a predefined intermediate position or not. Therefore, participants may have felt stimuli on the incorrect arm but still have disagreed that it had occurred at the position predefined by the experiment. In the present study, in contrast, we used measures that allowed direct assessment of whether wrong limb assignment did or did not occur.

Although it seems surprising that humans report stimuli presented on an arm to have occurred on a leg, previous studies have reported evidence for such confusion of limbs. These studies used manipulations of body posture, with arms and legs crossed over the midline. For instance, when participants have to indicate which of two tactile stimuli, one on a crossed hand and one on a crossed foot, occurred first, they often report the wrong limb (Schicke & Röder, 2006). Whereas in that paradigm, participants performed a forced choice between only the two options of “hand” and “foot”, a recent study reported that participants also chose an incorrect limb – and sometimes a foot for a hand and vice versa – when they had to assign a single stimulus to

one of the four limbs (Badde et al., 2019). Thus, our present results of arm/leg confusion are not without precedence and add to a growing body of evidence that the perception of where on the body a touch occurred can be categorically wrong.

Such errors in assigning touch to far distant limbs may seem dysfunctional. However, it is important to emphasize that the rabbit illusion is elicited by very unusual stimulus sequences that are designed to tickle out the dependence of perceptual processing on prior experience. In fact, there are other situations in which assigning tactile input to locations other than those at which they truly arise is highly functional: it is now well-established that humans are able to precisely localize where a tool they hold was touched (Heed, 2019; Miller et al., 2018, 2019), although, of course, the tactile input is sensed with the hand rather than the tool itself. Ultimately, the perception of touch on tools may well be forged by experience in the same way as our tactile perception on the body emerges from our lifelong interaction of objects with our skin (Miller et al., 2019). That the cutaneous rabbit is perceptually localized off the body when participants hold a pen between their stimulated fingers is, in our view, good evidence for such equivalence.

A Bayesian observer model fed with external distances replicates central aspects of the empirical data

The most elaborate model of tactile localization to date is the Bayesian observer model (Goldreich, 2007; Goldreich & Tong, 2013). This model predicts the perceived locations of stimuli based on localization variability and a prior that assumes single stimuli to result from a common object that slowly moves across the skin. Here, we applied the model to fit single participant data and tested whether participants' localization behavior was predicted by the model if we defined stimulus locations in external space and the distances between them as Euclidian distances. As predicted by the model, we observed larger displacements of the second stimulus in the illusory rabbit trials compared to no illusion sequences because of the different stimulus timings, which is the hallmark of the cutaneous rabbit effect.

Next, the Bayesian observer model predicts that rabbit effects should be more pronounced in body areas with low spatial acuity (Goldreich, 2007; Goldreich & Tong, 2013), a prediction that has been confirmed in multiple setups and paradigms (Geldard & Sherrick, 1983; Tong et al., 2016; Warren & Tillery, 2011). In our study, precision was higher on the arms than on the leg, consistent with earlier work (Mancini et al., 2014; Weinstein, 1968). Hence, the model predicted smaller displacement for stimuli on the arm than on the leg, which was partially confirmed by our experimental data. In line with this prediction, we observed stronger displacements of the second stimulus in a leg-to-arm than in an arm-to-leg direction. However, we did not find a significant difference when the single arm and the single leg configurations were compared with each other. The reason for the absence of this effect is not entirely clear. It is of note that the differences in precisions between arm and leg were also smaller when we compared the single limb configurations as opposed to the limbs in the two-limb configurations. It is possible that participants more efficiently compensated the perceptual imprecision in single limb configurations, potentially through attentional or expectation mechanisms, and that this diminished differences in rabbit patterns between the limbs.

Generally, there were strong positive relationships between predicted and observed positions indicating correspondence between the model and the data both in the single-limb and in the two-limb configurations. Therefore, the mechanisms that mediate the statistical integration of perceptual precision and a low-velocity prior are not restricted to single limbs, continuous skin stretches, or even the same cortical hemisphere. These results suggest the principal suitability of the model to prior experience made in external, Euclidian space.

However, the correspondence between predicted and observed localization was not perfect, and error patterns depended on the involved limbs. Specifically, a much larger displacement of the third stimulus towards the second was predicted by the Bayesian model than was observed in our experiment. Moreover, this discrepancy was most pronounced in the two-limb configurations. The fact that these model predictions were not met reverberates the above-mentioned suggestion that external-spatial priors alone do not fully capture the localization errors in the rabbit illusion paradigm. Future iterations of the Bayesian observer model could implement the currently disregarded anatomical factors to test whether localization can be fully explained by Bayes-like spatial integration across multiple spatial codes. At this stage, it is not quite clear how this anatomical prior could be defined. A straight-forward approach could be to integrate the Euclidian distances derived from external-spatial stimulus locations, as used in the present study, with 2D distances in skin space. Yet, the absence of any differences between the AL-1s and AL-2s configurations and the fact that the displacement of the second stimulus was quite accurately predicted by the model makes it unlikely that the missing anatomical prior relates to distance in 2D skin space. If the model lacked a 2D skin prior, rabbit effects should have been weaker in the AL-2s because the anatomical distance is larger in that limb configuration than in AL-1s. It is possible that the brain uses another, yet unknown prior, for example based on limb assignment (Badde et al., 2019; Maij et al., 2020), that increases the perceived distance between stimuli once the brain has inferred they had occurred on different limbs. This might be linked to recent Bayesian causal inference accounts (Debats et al., 2017; Kayser & Shams, 2015; Körding et al., 2007) which state that the process of (multi)sensory integration has two stages: in one process the brain infers whether stimuli should be integrated or segregated; in another process the brain computes the perceived features, for example perceived positions, for the case of integration and segregation. Although this framework is usually applied to multisensory integration, it is possible that the same principles applies for the integration of multiple sources of spatial information in unimodal tactile perception. This framework could also explain our finding that the illusion did not occur in all trials. This pattern could result from an inference process of perceptual segregation.

Limitations

Mislocalization in control sequences. High proportions of illusion-like responses in control sequences for the cutaneous rabbit effect have been observed before (e.g. Asai & Kanayama, 2012; Trojan et al., 2010; Warren et al., 2010). Our results showed that this phenomenon is accentuated on the leg compared to the arm. It is possible that our SOA of 700 ms was not sufficiently long to abandon the rabbit illusion completely. Note that in the study by Trojan and collaborators (2010) even at very long SOAs of up to one second there were still systematic displacements, although of smaller magnitude than observed here.

Attention. Whereas we interpret the stronger rabbit effects on single limbs as reflecting the influence of anatomical factors, a hypothetical alternative is that participants could focus attention better on the stimulus array in one than two arm configurations. This is because attentional focus is known to affect the perceived position of the second stimulus (Flach & Haggard, 2006; Goldreich, 2007; Kilgard & Merzenich, 1995). Generally, we attempted to minimize the influence of cognitive factors, such as attention and expectations about stimulus locations in our design. First, the stimulated limbs were placed under a cover during the whole session and, during preparation of the tactile stimulus array; we added dummy stimulators to prevent any visual anchor (Trojan et al., 2010). Second, we randomized the direction of stimulation (from limb 1 to limb 2 and vice versa) and employed multiple sequences so that focusing on one particular position of the array would not have had a consistent effect across trials (Goldreich & Tong, 2013). Moreover, we interspersed two-limb sequences with single-limb sequences to obscure when stimulation would cross limbs and when not. Overall, therefore, we do not consider attention a relevant factor for the result patterns we have presented.

Conclusion

In sum, we demonstrated cutaneous rabbit effects when stimulus sequences comprised two distant limbs and showed that the second stimulus of three can be perceptually displaced from the truly stimulated to the other involved limb. These findings suggest that the cutaneous rabbit illusion does not primarily reflect anatomical processing in the periphery and primary somatosensory areas, but instead relies on external-spatial priors that arise from life-long tactile interactions with objects in 3D space. Key aspects of human tactile localization behavior in the rabbit illusion are accounted for by a Bayesian observer model that is fed with stimulus distance in space, rather than along the skin. Nevertheless, stronger effects for stimulus contexts that involve only a single limb suggest that anatomical factors, too, play a role in the emergence of the rabbit effect. The existence of anatomical factors is consistent with early accounts of the phenomenon, and these factors may be critical to further improve a Bayesian integration account of tactile localization.

Material and methods

Experiment 1

Participants. We aimed to acquire 20 participants based on previous studies using similar methods that have recruited 15 to 20 (Eimer et al., 2005; Trojan et al., 2010, 2014). Of 21 acquire data sets, we had to exclude two, which left as well in the range of previous studies (13 females, mean age = 25 years, SD = 6). One participant was excluded due to technical problems, and one was excluded because (s)he was unable to maintain the required postures. All participants but one were right-handed, according to the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). They reported normal or corrected-to-normal vision and were free of any known neurological, visual, motor or tactile disorders. Participants were naïve about the purpose of the experiment and gave written informed consent prior to the experiment. They either participated without compensation or received course credit. The local ethics committee of Bielefeld University approved the experiment.

General procedures. Participants sat at a desk, in front of a computer screen. On the screen, a picture of a limb in the same position as the participant's limb(s) (Flach & Haggard, 2006) was displayed (Figure 10). All images had the same size and were mirrored for the configurations involving the respective other body side (see Table 3). Participants wore a cape both during setup and testing that prevented view of their stimulated limb(s) to reduce possible visual anchors (Trojan et al., 2010). Before each trial, there was a random inter trial interval, ranging between 1000 and 1500ms, during which a message on the screen indicated "Please focus on the touch". If participants indicated that they did not feel one of the stimuli, the experimenter pressed a key to repeat the trial at the end of the block. This happened rarely.

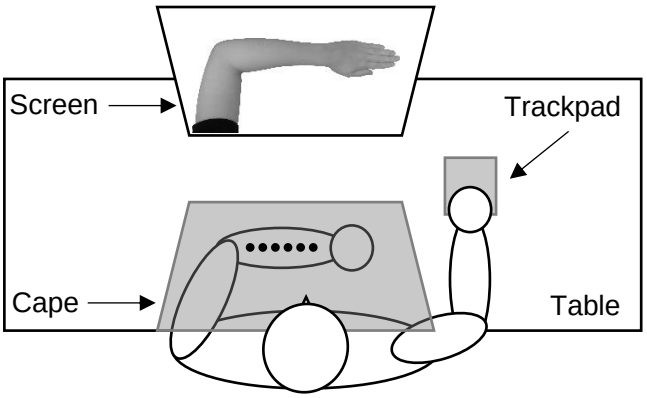

Figure 10. Experimental setup. *The schematic depicts the configuration "Left Single Arm" (see the following section for details of the other configurations).*

Depending on the task, one or three stimuli were presented to the participants' limb(s). Participants then localized each stimulus by clicking on the corresponding location on the screen using a trackpad. This reporting method allowed a direct measure of the rabbit percept and was similar to the one used by Flach & Haggard (2006). The trackpad was always placed so that it could be comfortably operated with a free hand, and whenever possible, with the dominant hand. The experiment with its five limb configurations lasted ~3 hours. As seen in Table 3, these configurations were divided in single limb configurations, involving either the arm or leg alone, and two-limb configurations. These configurations implied an arm and a leg (same or different body sides) or two arms. Half of the participants started with single limb configurations, the other half with two-limb configurations (order of the configurations was then randomized). There was a short break between each limb configuration. For each configuration, participants first performed a block of the single location task. Then the three stimulus sequences were presented in randomized order. In the single limb conditions, this resulted in 80 trials. In the two-limb configurations, we interspersed single-limb sequences, so that the trial number was 120, of which the 80 cross-limb trials were used in the analyses reported in the main text. In half of the participants, we stimulated the left body side in single limb conditions, and the right side in the other half of participants. At the end of the session, we asked the participants to judge the intensity of the stimuli perceived on the leg or on the arm using a visual scale, from zero (= no sensation) to ten (= very strong sensation). One stimulator was attached to the middle of each limb and participants rated its intensity. Participants judged the stimuli on the arm significantly stronger than on the leg (5.2 ± 2.0 vs. 3.0 ± 1.3; SE = .448, t = -4.93, p = .039).

Table 3. Images presented on the screen depending on limb configurations. *Participants performed each of the five configurations in a pseudo-randomized order (participants always performed all the single or the two-limb configurations first). Half of the participants performed with their right body side, half with the left.*

	Single Limb Configurations		Two-limb Configurations		
Body Side	Single arm (A)	Single leg (L)	Two arms (AA)	Arm Leg – two sides (AL-2s)	Arm Leg - one side (AL-1s)
Right					
Left					

Tactile stimuli. Eight solenoid vibrotactile stimulators (Dancer Design, St. Helens, UK; diameter 1.5cm) were connected to a custom-built control unit that was connected to the computer and ensured millisecond precision tactile stimulus timing. The experiment was controlled by the software PsychoPy (v1.85.6; Peirce, 2007). Each stimulus was a 45ms sine wave at a fixed output power for all stimuli. Participants wore headphones that played white noise to cancel any auditory noise from the stimulators. To determine stimulator positions on the arms and leg, we measured the participants' arm and leg length and marked the midpoint between wrist and elbow, as well as between ankle and knee. These lines were used to position casings that contained the stimulators, which were 1.5cm in diameter and placed 1.8 cm apart from each other. Once positioned, the stimulators were taped to the skin with adhesive tape rings and the casing removed. Six stimulators were used for the single limb configurations, and eight for the two-limb configurations (see Figure 1B). In particular, the stimulus arrangement avoided "crossing effects" (Heed & Azañón, 2014) that is, performance decrements when a stimulator on a left limb lies on the right of a stimulator of a right limb so that limb side and spatial position are incongruent. Preliminary testing for our experiments had indicated that such crossings could lead to confusing perception of the apparent movements for some participants. Stimulators were numerated from 1 to 8, always starting on the left (i.e. direction proximal-distal for the left limbs, and distal to proximal for the right ones; see Figure 1B). Additional dummy stimulators were attached to obscure which stimulators would be active during the experiment. There were ten dummy stimulators for the single limb postures and twelve for the two-limb (Figure 1A,B).

Stimulus sequences. In the first task, we used single location sequences. In the second task, we used three different stimulus sequences: illusory rabbit sequences, time control sequences, and location control sequences. Note, all trials of the three sequence types were randomized together and presented in one block. Illusory rabbit sequences were smaller in number as compared to the time control and location control sequences to obscure the aim of the experiment.

The *single location* consisted of one stimulus per trial, at any of the six or eight possible locations in a random order (respectively for numbers 1-6 for the single or 1-8 for the two-limb configurations, see Figure 1). Each position was repeated six times so that this block consisted

of 36 trials for each single limb configuration and 48 trials for each two-limb configuration. It was used to assess the localization independently of any spatiotemporal integration.

The *illusory rabbit* sequences consisted of three stimuli per trial, the first two at one location and the last at another at a distance of 10 cm (Trojan et al., 2010). Stimulus Onset Asynchrony (SOA) was 700 ms between first and second stimulus, and 100 ms between the second and the third (Eimer et al., 2005). We used six patterns for the single limb configurations (1-1-4, 2-2-5, 3-3-6, 6-6-3, 5-5-2, 4-4-1, see Figure 1A), and ten for the two-limb configurations (right body side: 1-1-4, 4-4-1, 8-8-5, 5-5-8, 1-1-6, 6-6-1, 2-2-7, 7-7-2, 3-3-8, 8-8-3; left body side: 1-1-4, 4-4-1, 8-8-5, 5-5-8, 2-2-5, 5-5-2, 3-3-6, 6-6-3, 4-4-7, 7-7-4; see Figure 1B). Note, that 4 of these 10 sequences were single limb sequences, such as 1-1-4 (see Figure 1B), and that left-to-right and right-to-left sequences were balanced. Each pattern was presented five times in randomized order, so that this condition comprised 30 trials for single limb configurations and 50 trials for two-limb configurations.

The *time control* sequences consisted of three stimuli per trial, similar to the illusory rabbit sequences. They were designed as control condition for the illusory rabbit sequences and stimulated the same positions, but with a 700 ms SOA between all stimuli to reduce the probability that participants would perceive the rabbit illusion (Trojan et al., 2010). Stimulus patterns, involved stimulators and repetitions were as for the illusory rabbit sequences.

The *location control* sequences were designed as another control sequence and also consisted of three stimuli per trial with 700 ms SOAs between all stimuli. However, instead of two, three distinct locations were stimulated, with the second stimulus located between the first and third. We included these trials so that participants felt three different locations not only when the rabbit illusion occurred, but also in other trials, again to obscure the aim of the experiment as well as to ensure that participants found it normal to report intermediate locations. Four types of patterns were used for the single limb configurations (1-2-4, 6-5-3, 4-2-1, 3-5-6) and four for the two-limb configurations (right body side: 1-7-6, 3-2-8, 6-7-1, 8-2-3; left body side: 2-3-5, 4-6-7, 5-3-2, 7-6-4). Each pattern was repeated five times, so this block consisted of 20 trials for each configuration. Here also, both proximal-distal and distal-proximal directions were equally represented.

Data processing. Raw data were pre-processed and analyzed with R (v3.6.1; RStudio v1.1.442; R Core Team, 2018). The coordinates of each location indicated by participants were recoded so that data were coded as if all participants had performed all configurations with their left body side, and the AL-2s configuration with their left arm and right leg. The Euclidean distance between the reported locations of the first and the third stimulus was then calculated, and the second perceived stimulus was projected on the line between the first and third. We computed the magnitude of the rabbit illusion as the percentage of shift of the second stimulus toward the third (see Figure 11). Participants sometimes confused the order or direction of the stimuli, for instance by reporting positions of stimuli 1, 3, 2 instead of 1, 2, 3). This kind of error has been frequently observed by others at similar rates (Asai & Kanayama, 2012; Trojan et al., 2014). We excluded trials with order or direction errors (23% of all trials) with a safety margin of 10%, resulting in the remaining trials having a proportion of displacement between -10% and 110%. We defined a threshold of 10% displacement above which we considered that the rabbit illusion was present. Other choices for this threshold did not lead to major changes in the result pattern;

see Supplementary File 1, Table S3 & Figure S2). According to this threshold, all displacements in the range of -10% to 10% were treated as if participants had reported the first and second stimuli in the same location and, thus, that the rabbit illusion had not occurred in the respective trial. Similarly, displacement of 100% would indicate that the second and third stimuli were perceived at the same location.

For the two-limb configurations, we used image masks to determine whether the second stimulus had been reported on the limb on which it had been presented, or whether it had been assigned to the other limb (Figure 11).

We did not analyze trials in two-limb configurations that involved only stimuli on a single limb.

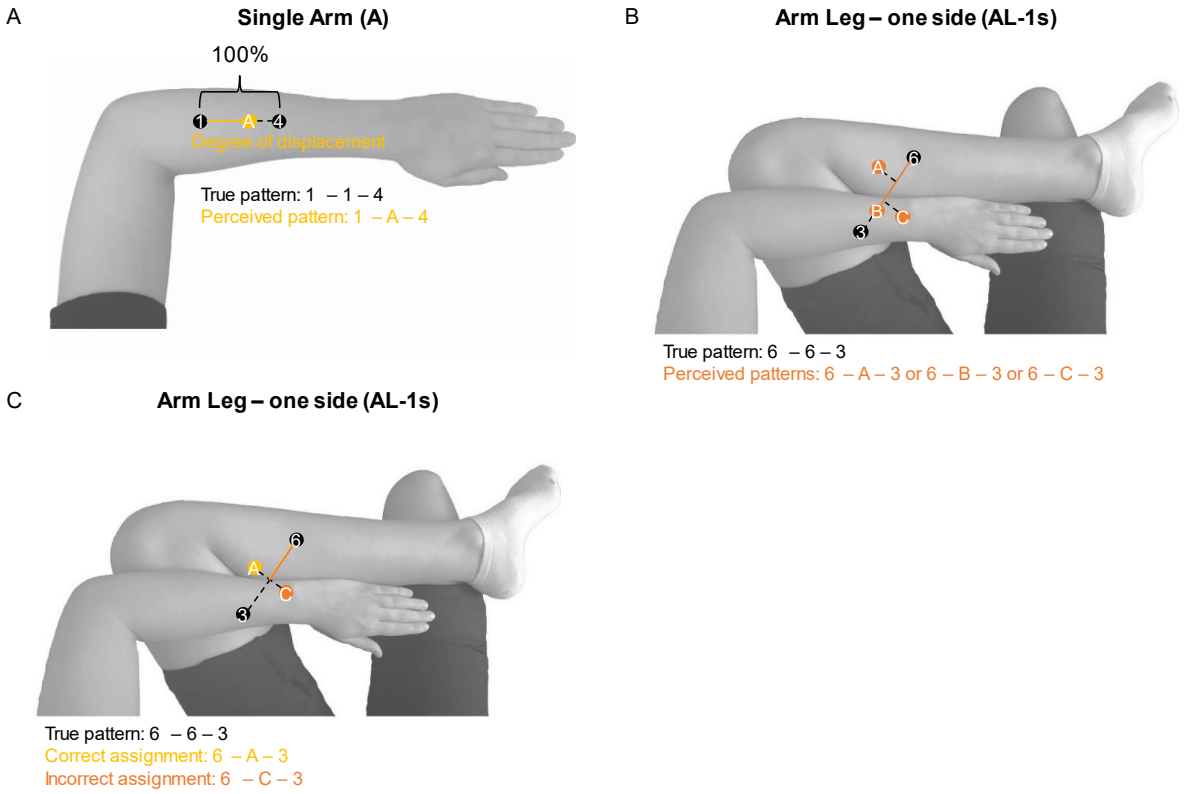

Figure 11. Schematic representation of the extracted measures, in single limb (A) and two-limb (B & C) configurations. *The degree of displacement (A & B) indicates how far the second stimulus was shifted towards the third. We considered the rabbit illusion as present when there was a displacement of the second stimulus > 10% of the distance between first and third stimuli. We further assessed whether the second stimulus was assigned on the correct limb, that is on the same as the first stimulus or not (C).*

Statistical analysis. (G)LMM. We used (Generalized) Linear Mixed Models ([G]LMM) for all statistical analyses, implemented in R (v3.6.1; RStudio v1.1.442; R Core Team, 2018) with the package lme4 (Bates et al., 2015). For each model, we implemented the maximum random effects structure for which the respective model still converged and improved model fit (Barr et al., 2013). We used the package car (Fox & Weisberg, 2011) to obtain statistics for main effects and interactions based on Type III Wald chi-square tests; we report these values rather than lme4 output). We performed posthoc tests and contrast analyses with the package emmeans (Russell, 2019), and adjusted the resulting *p-values* with the false discovery rate method for multiplicity adjustment.

Statistical analysis: single stimuli. Aside from familiarizing participants with the stimuli, we ensured with the single location trials analysis that participants could discriminate between the different stimulated positions. We ran a separate linear mixed model for each configuration with factor Stimulator (numbers 1-6 and 1-8, respectively, for single and two-limb configurations),

Statistical analysis: three-stimulus sequences. We performed separate comparisons of each control sequence type with the experimental rabbit illusion sequence type, because the two control sequence types were not compatible in one common analysis as the spatial locations varied between them. The time control sequences were designed as a comparison in which the first and second stimuli were in the same true location, but the expected percept differed from the experimental rabbit illusion sequences due to stimulus timing. The location control sequences were designed as a comparison in which the second stimulus was truly at an intermediate position between the first and third stimuli, that is, at a location at which the second stimulus may be perceived due to the rabbit illusion in the experimental sequences.

At some proportion of trials in both the rabbit illusion and time control sequences reported locations of the second stimulus were near the location of the first stimulus, and displacement was near 0 in our -10 to 110% proportional measure. This report indicates that participants did not experience the rabbit illusion, which is defined as the second stimulus being perceived displaced towards the third. Therefore, we used a two-part modeling approach (Sauzet et al., 2019).

In the first step, we assessed the presence or absence of the illusion in a given trial by classifying a trial as “illusion absent” when the reported displacement of the second stimulus was <10% and as "illusion present" otherwise. This analysis rendered the frequency with which the rabbit percept was evoked by the different sequence types. This step used a generalized linear mixed model with a binomial link function with factors *Limb Configuration* (A, L, AA, AL-1s, AL-2s) and *Stimulus Sequence* (illusory rabbit / time control or illusory rabbit / location control).

In the second step, we performed analyses on magnitude and limb assignment of only those trials that had been classified as “illusion present” in the first analysis step. Thus, step 2 assessed aspects of behavior only if the rabbit illusion had occurred. The first analysis assessed the degree of illusory displacement of the second stimulus as an indicator of the rabbit percept’s magnitude. We used a linear mixed model with factors *Limb Configuration* and *Stimulus Sequence* (illusory rabbit vs. time control). The second analysis assessed whether the second stimulus had been reported on the limb on which it had been presented, or whether participants reported this stimulus on the second limb. This effect could only occur in two-limb configurations, so that only the respective trials entered this analysis. We used a GLMM with a binomial link function with factors *Limb Configuration* (AA, AL-1s, AL-2s) and *Stimulus Sequence* (illusory rabbit / time control or illusory rabbit / location control).

Experiment 2

Participants. We recruited 21 new participants for Experiment 2, of which one was excluded due to technical problems. The remaining 20 participants (18 females, mean age=23 years, SD = 2.9) were all right-handed according to the EHI. Recruitment, inclusion, compensation procedures, and the laboratory setting were identical to those of Experiment 1.

General Procedures. The stimulation setup was similar to the left-arm-left-leg (AL-1s) configuration in Experiment 1, with identical positioning of the stimulators on the limbs (see Figure 1B). However, here participants performed a two-alternative force choice task (2AFC). Participants gave their responses with a two-button response box which they operated with two fingers of their dominant hand. Participants wore headphones to cancel any noise from the stimulators and to receive feedback tones during the task. The session lasted for 1.5 to 2 hours. At the end of the session, participants judged stimulus intensities for arm and leg with a visual scale that ranged from zero (= no sensation) to ten (= very strong sensation). As in Experiment 1, participants rated stimulation stronger on the arm than on the leg (6.6 ± 2.1 vs. 4.2 ± 2.0; SE = .483, t = -4.99, p = .002).

Stimulus Sequences. Stimulation patterns were identical to the two-limb sequences of Experiment 1, with illusory rabbit, time control and location control sequences. For illusion and time control sequences, the first and second stimuli were presented on one limb, and the third on the other, just as in Experiment 1. Thus, the positions for the illusory rabbit and time control sequences were: 2-2-5, 3-3-6, 4-4-7, 5-5-2, 6-6-3, 7-7-4 (see Figure 1B). The positions for the location control sequences were: 3-5-6, 4-6-7, 5-3-2, 6-4-3, 2-3-5, 3-4-6, 6-5-3, 7-6-4. Each illusory rabbit pattern was repeated 50 times and each time control and location control pattern 25 times. In total, the experiment comprised 650 trials (300 illusory rabbit, 150 time control, and 200 location control trials). Sequence order was randomized and split into blocks of 50 trials. Participants took breaks after each block.

2AFC task. Following the stimulus sequence, participants had to decide on which limb they had perceived *two* stimuli. They indicated their decision with response buttons. Assignment of limb to response buttons was counterbalanced over the participants. The task directly assessed whether the second stimulus was incorrectly assigned to the other limb, that is, whether it "jumped" form the truly stimulated limb to the other in the stimulus percept. As an example, think of a trial in which the first two stimuli were presented on the leg and the third on the arm. The first and third stimuli were almost always reported on their correct limb in Experiment 1. Therefore, if the participant now indicated that (s)he perceived two stimuli on the arm, then (s)he must have perceived the second stimulus on the arm along with the third. Given that the second stimulus was always presented at the position of the first stimulus – here, the leg –, this response indicates that the second stimulus has been incorrectly localized to the arm. In other words, the second stimulus "jumped" from one limb to the other. Participants were instructed to prioritize responding correctly over speed, but to press the button as soon as they were sure about their response. The beginning of each trial was indicated by a beep (880 Hz, 100 ms). This was followed by a random interval of 100-500 ms, after which the stimulus sequence was presented. When participants did not respond within a 3000 ms time limit, measured relative to the offset of the last stimulus, a tone (440 Hz, 200 ms) reminded them to respond faster. Finally, a 1200 Hz tone feedback indicated that a response was considered invalid; this was the case if the response had occurred too fast (response time <100 ms after the sequence end; tone duration 100 ms) and if multiple button presses were registered (tone duration 200 ms). No-response and invalid trials were repeated at the end of a block.

After each trial, the program evaluated whether the response was correct and determined whether a confidence rating was shown. The inter trial interval was 500 ms if no confidence rating was presented.

Confidence ratings. We presented confidence ratings after some trials to assess how certain participants were about correct and incorrect choices. In Experiment 1, the rate of incorrect limb assignment was around 35 %. Therefore, we increased the number of trials in Experiment 2 so that we would be able to reliably observe the phenomenon here as well. To keep the experimental time low, we did not assess confidence after every trial but instead interspersed them randomly. A confidence rating was shown with a probability of 80% after an incorrect response, that is, when the response indicated that the second stimulus had been assigned to the incorrect limb. After correct responses, a rating was shown with a probability of 20%. This seemingly unbalanced sampling was chosen to assess similar amounts of ratings for correct and incorrect choices, with incorrect choices occurring less frequently and, therefore, being sampled with higher probability.

Confidence ratings had two phases. The participant was first asked, via text on the computer screen, whether the last button press had been correct. Yes/no responses were given by clicking on one of two buttons presented on the screen using the mouse. If the participant responded no, then the rating was not evaluated further. If the participants responded yes, a confidence rating asked the participant how certain they were about their assignment on which limb they had perceived two stimuli. Participants adjusted a continuous slider on the screen that indicated 0, 50 and 100% landmarks. 100% meant that the participant was absolutely certain of their response; 0% meant that they were maximally uncertain. The slider was controlled by grabbing it with the computer mouse. The currently selected value (between 0 and 100) was shown underneath, and participants confirmed their rating by clicking on the number below the scale. Both the yes/no response and the slider response was unspeeded and did not have a time limit. After the confidence rating was completed, there was an inter-trial interval of 2000 ms to give participants sufficient time to remove the hand from the mouse and back to the response buttons before the next stimuli were presented.

Statistical analysis. As in Experiment 1, we ran separate analyses to compare illusory rabbit vs. time control and illusory rabbit vs. location control sequences. We devised three analyses. First, we assessed the probability of an incorrect response – indicative of a stimulus reported on the wrong limb – with a GLMM with a binomial link function with factor *Stimulus Sequence* (illusory rabbit / time control or illusory rabbit / location control).

Second, we analyzed only those trials in which participants had given a confidence rating and indicated that they believed they had been correct (94% of the trials with a confidence rating). We examined differences in confidence ratings across the experiment's conditions with a LMM with factors *Stimulus Sequence* (illusory rabbit / time control or illusory rabbit / location control) and *Accuracy* (correct, incorrect).

Finally, we investigated whether accuracy in Experiment 2 could be fully explained by confidence ratings. The underlying logic of this analysis was that localization errors would simply express uncertainty and, possibly, guessing, if differences across conditions are accounted for by confidence. In contrast, if confidence cannot explain our experimental data,

then the rabbit illusion must originate from other factors than uncertainty. We ran a GLMM with a binomial link function with factor *Stimulus Sequence* and a continuous covariate *Ratings*. The proportion of errors in control trials was quite low; therefore, we excluded the interaction between the two factors. Analysis tools and analysis strategies were otherwise identical to those reported for Experiment 1.

Bayesian observer model

Reformulation of the model for three, rather than two, stimuli. We adopted the Bayesian observer model by Goldreich and Tong (2013). The general logic of the Bayesian observer model for two stimuli is that the observer infers a movement trajectory (x_1, x_2) based on information about sensed (or "measured") positions (x_{1m}, x_{2m}), the time (t) that passed between them, the spatial uncertainty of each sensed position (σ_1, σ_2) and an assumption of low velocity (σ_v) that expresses the observer's expectation of change in spatial units per one temporal unit. The presumed origin of the low velocity prior is the typical, average speed with which objects move along our skin during our every-day life.

Using Bayes's theorem, the Bayesian observer model predicts the perceived positions computed as the mode of the posterior distribution, which is a two-dimensional Gaussian distribution with one dimension corresponding to x_1 and the other to x_2 when only two stimuli are involved.

In analogy, when the Bayesian observer model is extended to three stimuli, the resulting posterior distribution is a three-dimensional Gaussian. For three stimuli, the model integrates not only one, but two, time intervals: t_1 as the interval between the first and the second stimuli and t_2 as the interval between the second and the third stimuli. The posterior distribution is computed as described in Equation 1.

$$p(x_1, x_2, x_3 | x_{1m}, x_{2m}, x_{3m}, t_1, t_2) \propto \exp\left(-\left(\frac{(x_{1m}-x_1)^2}{2\sigma_1^2} + \frac{(x_{2m}-x_2)^2}{2\sigma_2^2} + \frac{(x_{3m}-x_3)^2}{2\sigma_3^2} + \frac{(x_2-x_1)^2}{2(\sigma_v t_1)^2} + \frac{(x_3-x_2)^2}{2(\sigma_v t_2)^2}\right)\right) \quad \text{(E1)}$$

In E1, x_{im} denotes the sensed positions of stimulus 1-3; σ_i their standard deviations, that is, the inverse of spatial precision, t_1 and t_2 the time intervals between stimuli (1, 2) and (2, 3), respectively; σ_v the low velocity prior; and x_i the true positions of the stimuli that the model attempts to infer given data and the prior assumption. The most likely configuration of x_i, given the other parameters, is defined by the posterior mode and corresponds to the percept that the model predicts.

The configuration of x_i corresponding to that mode can be computed analytically by taking partial derivatives for each x_i, setting them to zero, and solving the resulting system of three linear equations (for details see Goldreich & Tong, 2013).

Computation of model parameters. The model requires estimations of baseline localization precision for each of the stimulus localization as an estimate of σ_i. We computed average localization as centroids and the distribution of localization error around it as the estimates for the σ_i for each participant and limb configuration. We estimate centroids in the context of the experiments three-stimulus sequences. For each stimulator, we averaged localization over all

trials in which a sequence had begun with the stimulator of interest, because the first stimuli in our sequences were usually not subject to illusory displacement.

To derive a single precision measure, we averaged standard deviations in x and y direction. We then averaged the variability values for all stimulators to derive a single variability estimate per limb but determined separate values for each of our Experiment 1's limb configurations.

The Bayesian observer model is specified for only a single dimension. Therefore, we reduced localization responses in the illusory rabbit and time control stimulus sequences to one dimension by projecting participants 2D localization responses onto a straight line between locations of stimuli 1 and 3. We derived these locations from the centroids, described in the last paragraph. This procedure is similar to the calculation of the attraction index we computed to derive the amount of illusory displacement (see section *Data processing*) with the difference that in the present case we used the straight line between the centroids and not the localizations in the respective trial. Last, we transformed the data into approximate cm units. This step was necessary because the model's low-velocity prior (σ_v) is expressed as a value in cm/s in the literature, e.g. 10 cm/s (Goldreich, 2007; Goldreich & Tong, 2013) and would not be transferable to the pixel units that we used for our localization. We computed a transformation from pixel to cm units for each participant, based on the fixed distance of 10 cm between the first and third stimuli for all our experimental sequences, independent of limb configuration. The distances between the centroids of these stimulators should, on average, be close to 10 cm. We therefore averaged the distances between the first and the third stimuli of each respective limb configurations, expressed in pixel values, as an estimation of a 10 cm distance. This estimation divided by 10 expresses the number of pixels corresponding to 1 cm. Accordingly, we transformed the projections on the straight line into cm units by dividing them by the number of pixels corresponding to 1 cm. These values corresponded to the x_{im}. Using the same transformation, also the σ_s were transformed into cm units.

We then computed model predictions for each participant in all configurations and stimulus patterns using the x_{im} and σ_s. For the illusory rabbit sequences, we used a t_1 parameter of 0.7 s and a t_2 parameter of 0.1 s. For the time control trials we used a value of 0.7 s for both intervals. For both sequences, we used a low-speed prior set to 10 cm/s, as suggested in previous studies (Goldreich, 2007; Goldreich & Tong, 2013).

Statistical analysis. We assessed model performance in four ways. First, we compared variability for arms and legs. Because the number of involved levels of *Limb* varied between single-limb (only one limb) and two-limb configurations (two limbs), we analyzed them separately. We assessed the A and L configurations with an LMM with fixed factor *Limb Configuration*. We assessed AA, AL-1s and AL-2s in a second LMM with fixed factor *Limb Configuration* and *Limb* (limb 1 and limb 2 of the respective configuration).

Second, we focused on the model's predictions about the displacement of the second stimulus on the leg compared to the arm in the illusory rabbit stimulus sequence. We compared the observed positions of the second stimulus in the A and L in the illusory rabbit sequence with an LMM with fixed factor *Limb Configuration*. We analyzed AL-1s and AL-2s with an LMM with fixed factors *Limb Configuration* and *Direction* (stimulus sequence moving arm-to-leg vs. leg-to-arm).

Third, we regressed predicted onto observed positions to assess how well the model predicted the observed positions generally and whether this general fit differed between single-limb and two-limb configurations. We restricted regressions to the second and the third stimuli of our sequences, because these are typically mislocalized in three-stimulus rabbit sequences. We omitted the first stimulus of the sequences from analysis, because participants usually localized this stimulus quite well, and so including this stimulus would have positively, but artificially, affected model assessment. To test for differences between single-limb and two-limb configurations, we grouped configurations into a factor *Limbs* (one vs. two). One level included the A and L; the other the AA, AL-1s and AL-2s limb configurations. We included the model's predicted positions as a continuous predictor.

Fourth, we analyzed whether the Bayesian model also predicted observed positions locally, i.e., when looking at the second and third stimuli separately. This was done because the Bayesian model is inherently informed about the true location of the stimulus 2 at 0 and stimulus 3 at 10 cm and this information can already explain a large proportion of the variance. However, the model should even be able to explain the variation seen within each of the second and the third stimuli. To test this prediction, we computed another LMM including the predicted values and the fixed factors *Limbs* and *Stimulus* (second vs. third). The model was restricted to the data of the illusory rabbit pattern because the variation within stimuli was restricted for the time control pattern which does not permit regression analyses.

Acknowledgements

This work was supported by the German Research Foundation (DFG) through the Cluster of Excellence Cognitive Interaction Technology 'CITEC' at Bielefeld University, and an Emmy Noether grant to TH (He 6368/1-3). We thank Nele Rödenbeck and Sarah Bremsteller for their support with data acquisition, and Odile Sauzet for statistics consulting.

Competing interests

There are no conflicts of interest.

Data availability statement

All data and code used in this study are available on the website of the Open Science Framework (OSF) and can be accessed at https://osf.io/a8bgt/.

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