Sharpened self-other distinction in attention deficit hyperactivity disorder

Rebecca Bohmea,d,⁎, Morgan Frost Karlssona, Markus Heiliga,b,d, Håkan Olaussona,c,d, Andrea Johansson Capusan,a,b

a Center for Social and Affective Neuroscience, Linköping University, Department of Biomedical and Clinical Sciences, 58185 Linköping, Sweden
b Department of Psychiatry, Linköping University, 58185 Linköping, Sweden
c Department of Clinical Neurophysiology, Linköping University Hospital, 58185 Linköping, Sweden
d Center for Medical Imaging and Visualization, Linköping University, 58185 Linköping, Sweden

ARTICLE INFO
Keywords:
ADHD
Social touch
Self-other-distinction
Bodily self
fMRI
Rubber hand illusion

ABSTRACT
Introduction: Differentiation between self-produced tactile stimuli and touch by others is necessary for social interactions and for a coherent concept of “self”. In attention-deficit-hyperactivity-disorder (ADHD), tactile hypersensitivity and social cognition problems are part of the symptomatology, but pathophysiological mechanisms are largely unknown. Differentiation of self- and non-self-generated sensations might be key to understand and develop novel strategies for managing hypersensitivity. Here, we compared the neural signatures of affective self- and other-touch between adults with ADHD and neurotypical controls (NC).

Methods: Twenty-eight adult ADHD participants and 30 age- and gender-matched NC performed a self-other-touch-task during functional magnetic resonance imaging: they stroked their own arm, an object, or were stroked by the experimenter. In addition, tactile detection thresholds and rubber hand illusion (RHI) were measured.

Results: ADHD participants had more autistic traits than NC and reported to engage less in interpersonal touch. They also reported to be more sensitive to tactile stimuli. Compared to NC, ADHD participants showed enhanced responses to both the self- and other-touch conditions: stronger deactivation during self-touch in the anterior and posterior insula, and increased activation during other-touch in primary somatosensory cortex. ADHD participants had intact tactile detection thresholds, but were less susceptible to the RHI.

Conclusions: Unaltered detection thresholds suggest that peripheral processing is intact, and that hypersensitivity might be driven by central mechanisms. This has clinical implications for managing somatosensory hypersensitivity in ADHD. The more pronounced differentiation between self- and other-touch might indicate a clearer self-other-distinction. This is of interest regarding body ownership perception in both NC and ADHD, and possibly other psychiatric conditions with altered self-experiences, like schizophrenia. A sharper boundary of the own body might relate to deficits in social cognition and tactile hypersensitivity.

1. Introduction

Attention-deficit/hyperactivity disorder (ADHD) is characterized by inattention, impulsivity and hyperactivity. ADHD is typically diagnosed during childhood but often persists into adulthood. ADHD can negatively affect life outcomes in multiple areas, e.g. in social interaction, education and occupation (Faraone et al., 2015).

ADHD is associated with a higher prevalence of depression, anxiety, substance use disorder and autism spectrum disorder (ASD) (Garcia et al., 2012). In ASD, sensory abnormalities like hyper- and hypo-sensitivity have been described (Baron-Cohen et al., 2009). Much less is known about sensory processing in ADHD. The few available studies in children point to a sensory processing dysfunction (Ghanizadeh, 2011; Shimizu et al., 2014; Yochman et al., 2004), which seems comparable to that of children with ASD (Little et al., 2018). In children with ADHD, about 50% have increased somatosensory reactivity in multiple sensory domains, compared to 20% in typically developing children (Lane et al., 2010). In adults with ADHD, auditory hypersensitivity is related to inattention severity (Micoulaud-Franchi et al., 2015) and increased pain sensitivity (Treister et al., 2015). Atypical sensory processing is not related to the amount of autism traits, but to self-reported ADHD symptoms (Bijlenga et al., 2017), indicating that sensory dysfunction

⁎ Corresponding author at: Center for Social and Affective Neuroscience, The Department of Biomedical and Clinical Sciences, Linköping University, S-581 83 Linköping, Sweden.
E-mail address: Rebecca.bohme@liu.se (R. Bohme).
should be considered as a key symptom domain in ADHD. Even in the general population, ADHD traits relate to altered self-reported sensory sensitivity (Panagiotidi et al., 2018). Altogether, this suggests that sensory hypersensitivity plays an important role for attention deficits in ADHD.

Most studies on hypersensitivity in ADHD involve children and rely on self-report or parent-report; few studies have tested hypersensitivity experimentally. Such studies suggest differences in tactile adaptation (Puts et al., 2017) and in physiological measures of recovery from a sensory challenge (Lane et al., 2010). While one study found higher tactile detection thresholds – possibly related to inattention – (Puts et al., 2017), another found no difference between children with ADHD
Sensory processing problems relate to sleep and behavior problems in ADHD (Molagholamreza Tabasi et al., 2016; Shochat et al., 2009). Furthermore, tactile hypersensitivity can have far reaching consequences for affected people, from leisure activities (Engel-Yeger and Ziv-On, 2011) to food preferences (Nederkoorn et al., 2019, 2015). Considering the importance of social touch during development (McGlone et al., 2014), hypersensitivity to touch by others might relate to social problems in ADHD, as has been suggested for ASD (Carissa J Cascio et al., 2018). However, somatosensory processing, especially social touch, has hardly been studied in the ADHD population, and particularly not in adults. Symptomatology, comorbidities and subtypes might differ between adults and children (Faraone et al., 2015, 2006; Moffitt et al., 2015). Therefore, we studied the processing of social touch stimuli in young adults with ADHD.

Adult ADHD participants and matched controls performed the self-other-touch-task previously established in neurotypical people (Boehme et al., 2019). Participants stroked their own arm (self-touch condition) or were stroked by the experimenter (other-touch condition). We used functional magnetic resonance imaging (fMRI) and psychophysics to measure behavioral and neurophysiological processing of self-touch and other-touch. Based on previously reported hypersensitivity problems, we hypothesized that the psychophysical test of ADHD participants would show lower detection thresholds for weak tactile stimuli.

With regard to fMRI, we hypothesized that ADHD participants would be more sensitive to non-self-generated sensations, accompanied by a sharper self-other-distinction. Our region of interest here was the insula, given studies showing that posterior insula activates in response to slow stroking social touch (Morrison et al., 2011; Olausson et al., 2008) and plays a role in body ownership (Tsakiris et al., 2007), while anterior insula has been implicated in integrating interoceptive signals (Kirsch et al., 2020), in the awareness of the own body (Craig, 2002, 2009; Karnath and Baier, 2010) and in tracking mismatches between predicted and actually perceived sensations (Allen et al., 2016).

A clearer self-other-distinction might in turn sharpen the experienced bodily self (Fotopoulou and Tsakiris, 2017; Gallagher, 2000; Gallagher and Meltzoff, 1996). A way to test the stability of one’s own body are body ownership illusions, like the rubber hand illusion (RHI) (Tsakiris et al., 2006). Since we hypothesized that ADHD participants exhibit a clearer self-other-distinction, we expected them to be less susceptible to the RHI.

2. Methods and materials

The study consisted of two parts: the first part was a functional magnetic resonance imaging (fMRI) session and the second part included detection thresholds and rubber hand illusion (RHI).

2.1. Participants

Exclusion criteria for the neurotypical controls (NC) were any psychiatric disorder, alcohol or substance abuse, chronic pain, or any other major health concern as assessed during a structured telephone interview.

Clinically stable ADHD participants were recruited at their biannual routine checkup visit at the adult Psychiatric Clinic, at the Linköping University Hospital, Sweden. Exclusion criteria for the ADHD group were any severe acute psychiatric disorders (such as, but not exclusively, psychosis, bipolar disorder, severe obsessive-compulsive disorder), ASD, substance use disorder within the past year, chronic pain or any other major health concern. In total, 53 adults with ADHD expressed interest in the study. Of these, five could not be reached, four declined participation after detailed study description, six were excluded for reasons related to MR scanning (metal in the body, claustrophobia), one due to ASD diagnosis, and one’s age was outside our target age range. Furthermore, seven participants did not show up for their appointment and one did not finish the fMRI task. The 24 persons not included had mean age 28.3 ± 5.0 years, 12 females (Fig. 1).

Some individuals with ADHD who could not participate in the first part due to MRI contraindications were able to participate in the second part, resulting in two partially overlapping samples.

Functional imaging data were thus obtained from 28 adults with ADHD (25.7 ± 4.7 years old, 15 females). 30 neurotypical adults were recruited as age- and gender-matched controls (23.7 ± 3.6 years old, 16 females). After fMRI, the participants filled out the Social Touch Questionnaire (Wilhelm et al., 2001), the Autism Quotient (Baron-Cohen et al., 2001), and the Empathy Quotient (Baron-Cohen and Wheelwright, 2004).

The majority (23 of 28 [82%]) took stimulant medication, two had medication with atomoxetine, and two had no medication for ADHD. ADHD volunteers were asked to refrain from taking stimulant medication for 48 h prior to participation. Four individuals with ADHD were on medication with antidepressants (SSRI), which they continued during the experiment.

All fMRI participants were contacted and asked to participate in the study’s second part. Threshold detection data was collected for 14 ADHD participants (26.7 ± 5 years old, 5 female) and 15 NC (24.9 ± 3 years old, 7 female), rubber hand illusion (RHI) data were obtained for 10 ADHD participants (24.1 ± 4.5 years, 6 female) and 15 NC. These samples contained two newly recruited ADHD participants and eight newly recruited NC (Table 1). These ADHD participants also took stimulant medication, from which they refrained for 48 h prior to the experiment. During phone contact for the second appointment, participants answered a questionnaire about their tactile sensitivity, based on the Sensory Perception Quotient (Tavassoli et al., 2014) and the Sensory Profile (Dunn, 1999; Dunn and Bennett, 2002).

The Linköping Regional Ethics Review Board approved the study (Dnr 2016/360-31, 2019-02318), and written informed consent was obtained after complete study description.

2.2. Self-other-touch task

Participants performed the self-other-touch task as described before (Boehme et al., 2019). In short, the task consists of three conditions: 1) self-touch, during which participants stroked their own left forearm with the right hand; 2) object-touch, where participants stroked a pillow with the right hand; 3) other-touch, where participants were stroked on the left forearm by the experimenter. Participants were instructed to perform slow, light stroking. Our main interest was the difference between self-touch and other-touch. The object-touch was a control for movement during self-touch.

2.3. fMRI

During fMRI, participants performed the touch task lying comfortably in a 3.0 Tesla Siemens scanner (Prisma, Siemens, Erlangen, Germany) with their left arm placed on their belly and the right arm propped up by pillows, to reduce the movement during self-touch.

The participants watched a computer screen through goggles, where they could read the task instruction and the cues for the upcoming trial. The cues were presented for three seconds (in Swedish): “Active, please stroke your arm”; “Active, please stroke the object”; “Passive, your arm will be stroked by the experimenter”. When the text turned green, the participant was stimulated or had to perform the stimulation while the text was on the screen, i.e. during a period of twelve seconds. The experimenter was standing next to the scanner bore and received auditory...
cues on when to perform the stroking action via headphones. In order to provide a comparable tactile stimulation during the self- and the other-touch condition, as our previous study evaluated using hand tracking, the experimenter watched the self-stroking motion that the participant was doing and mimicked it as closely as possible (Boehme et al., 2019).

Table 1

<table>
<thead>
<tr>
<th>MRI</th>
<th>Neurotypical controls</th>
<th>ADHD</th>
</tr>
</thead>
<tbody>
<tr>
<td>age (m, sd)</td>
<td>23.73 (3.61)</td>
<td>25.68 (4.73)</td>
</tr>
<tr>
<td>sex (N)</td>
<td>f: 16; m: 14</td>
<td>f: 15; m: 13</td>
</tr>
<tr>
<td>education level (N)</td>
<td>university: 25; high school: 1</td>
<td>university: 6; high school: 1</td>
</tr>
<tr>
<td>smoking (N)</td>
<td>yes: 0; no: 25; no answer: 2</td>
<td>yes: 5; no: 18</td>
</tr>
<tr>
<td>EQ (m, sd)</td>
<td>48.31 (14.01)</td>
<td>49.14 (12.62)</td>
</tr>
<tr>
<td>AQ (m, sd)</td>
<td>14.23 (9.08)</td>
<td>19.5 (8.87)</td>
</tr>
<tr>
<td>STQ (m, sd)</td>
<td>28.00 (9.47)</td>
<td>26.95 (13.47)</td>
</tr>
<tr>
<td>Tactile sensitivity (m, sd)</td>
<td>42.29 (6.06)</td>
<td>50.75 (8.69)</td>
</tr>
</tbody>
</table>

Detection Threshold

<table>
<thead>
<tr>
<th>MRI</th>
<th>Neurotypical controls</th>
<th>ADHD</th>
</tr>
</thead>
<tbody>
<tr>
<td>age (m, sd)</td>
<td>24.87 (3.02)</td>
<td>26.71 (5.01)</td>
</tr>
<tr>
<td>sex (N)</td>
<td>f: 7; m: 8</td>
<td>f: 6; m: 8</td>
</tr>
<tr>
<td>education level (N)</td>
<td>university: 15; high school: 0</td>
<td>university: 3; high school: 0</td>
</tr>
<tr>
<td>smoking (N)</td>
<td>yes: 0; no: 0; no answer: 7</td>
<td>yes: 3; no: 7; no answer: 4</td>
</tr>
<tr>
<td>AQ (m, sd)</td>
<td>13.71 (8.93)</td>
<td>18.10 (6.94)</td>
</tr>
<tr>
<td>EQ (m, sd)</td>
<td>47.86 (13.56)</td>
<td>42.36 (13.43)</td>
</tr>
<tr>
<td>STQ (m, sd)</td>
<td>28.00 (9.47)</td>
<td>26.95 (13.47)</td>
</tr>
<tr>
<td>Tactile sensitivity (m, sd)</td>
<td>42.87 (4.99)</td>
<td>51.54 (10.99)</td>
</tr>
</tbody>
</table>

Results

3.1 Participant characteristics

ADHD participants (Table 1) displayed reduced social abilities: they had more autistic traits (T = 4.2, p < 0.001) and lower empathy scores (T = 2.6, p = 0.012). They also differed in touch-behavior: ADHD participants reported to enjoy interpersonal touch less (T = 2.8, p = 0.006) and displayed more tactile hypersensitivities (T = 3.6, p = 0.001).

In NC, the amount of autistic traits was negatively correlated to empathy scores (r = -0.64, p < 0.001) and positively correlated to tactile hypersensitivities (r = 0.51, p = 0.02). We found no such associations in the ADHD group (AQ-EQ: r = -0.15, p = 0.48; AQ-sensitivity: r = -0.13, p = 0.61).
3.2. BOLD signal related to self- and other-touch

We were interested in group differences in BOLD signal in response to self-touch and other-touch. There was no main group effect. Both groups showed a higher activation for other-touch than for self-touch in superior and middle temporal gyrus, amygdala, anterior cingulate gyrus, claustrum, prefrontal and cerebellar regions (Fig. 2, Tables S2 & S3). The whole-brain comparison of the other-touch condition revealed that ADHD participants showed a stronger activation in the right primary somatosensory cortex (Fig. 3A), while there was no difference for the whole-brain group comparison during self-touch.

With respect to our ROIs, anterior and posterior insula, we found a group*condition interaction (Fig. 3B). To understand this interaction better, we performed a post-hoc test comparing groups separately for self-touch and for other-touch. The interaction was mainly driven by the self-touch condition, during which ADHD participants showed a stronger deactivation than NC (Fig. 3C). There was no group difference in the insula ROIs during other-touch.

3.3. Detection threshold

To see if the ADHD group was more sensitive to tactile stimuli, we compared stimulus detection thresholds between groups for a tactile stimulus that occurred either alone or simultaneously with our three touch conditions. In NC we found a difference between the four conditions (baseline, self-touch, other-touch, object-touch) using a Kruskal–Wallis ($\chi^2(3) = 29.8, P < 0.001, \text{Fig. 4}$). A post hoc Wilcoxon signed-rank test showed that detection thresholds during self-touch were significantly higher than during baseline and object-touch, (baseline: $Z = -3.4, P < 0.001$; object: $Z = -3.4, P < 0.001$), but not higher than during other-touch ($Z = -0.25, P = 0.8$). ADHD participants did not differ from NC in detection thresholds (repeated measures ANOVA: between subjects effect: $F(1,24) = 0.5, p = 0.49$) and there was no interaction between group and condition ($F(1.85,44.36) = 0.92, p = 0.4$).

3.4. Rubber hand illusion

NC reported to experience the illusion during synchronous stroking (mean rating $= 7.6 \pm 1.8$), but not during asynchronous stroking, which is considered a control condition (mean rating $= 2.7 \pm 1.9$). ADHD participants were less susceptible to the RHI during synchronous stroking (mean rating ADHD $= 5.1 \pm 1.5, T = 3.58, p = 0.002$). There was no difference between groups during asynchronous stroking (mean rating ADHD $= 3.4 \pm 3, T = 0.7, p = 0.48$).

4. Discussion

This is, to our knowledge, the first study to investigate responses to social touch in adults with ADHD. We found a clearer difference between processing of self-touch and social (other) touch in ADHD and that the ADHD group was less susceptible to the RHI illusion. Both these findings might indicate a clearer self-body-boundary. Detection thresholds did not differ between groups. This finding suggests intact peripheral detection of tactile stimuli in ADHD, while central processing might be altered.

The suggestion of a sharper self-other-distinction in ADHD is based on two observations: a stronger deactivation in the insula during self-touch and a stronger activation in the primary somatosensory cortex during other-touch. The stronger deactivation during self-touch might be related to stronger predictions about the sensory consequences of own actions resulting in an increased attenuation of self-generated stimuli (Blakemore et al., 1998). Typically, the brain seems to attenuate the sensations arising from one’s own actions, as they are behaviorally irrelevant. This is thought to work through an efference copy of the outgoing motor command, which predicts its sensory consequences (Von Helmholtz, 1867). This mechanism is important in detecting surprise, i.e. unpredicted sensations which might indicate a threat (e.g. an injury) or a reward (e.g. a positive social interaction). The anterior insula has been implicated in this mechanism through ascending input from thalamus and bidirectional functional connectivity with the primary somatosensory cortex. Furthermore, anterior insula might compare actual sensations with predicted sensations, identify mismatches and direct attention/awareness (Allen et al., 2016; Menon and Uddin, 2010). In line with this, anterior insula activates when detecting surprising tactile events (Allen et al., 2016). In the present study, we examined the opposite effect: a highly predictable tactile sensation during self-touch. Deactivation of anterior insula in both groups might indicate that there is no mismatch between predicted and perceived tactile sensation. In ADHD, we observed increased insular deactivation only during this highly predictable event. Considering a possible sensory overload in ADHD, this could an overcompensation: a stronger suppression of stimuli that a person with ADHD is hypersensitive to – if they are predictable, like in the case of self-touch.
Future studies should investigate developmental trajectories of sensory attenuation in ADHD (Martel et al., 2012; Moffitt et al., 2015).

An alternative interpretation could be that people with ADHD show stronger attenuation of self-produced stimuli because they experience a clearer bodily self with sharper boundaries, as has been suggested for people with ASD (Mul et al., 2019) – which could in turn lead to clearer efference-copy based predictions.

Our finding, of a heightened activation in the primary somatosensory cortex in response to other-touch, might relate to somatosensory hypersensitivity and alterations in social interaction behavior. This hypersensitivity to touch is in line with previous reports of sensory over-reactivity in ADHD (Lane et al., 2010; Micolaud-Franchi et al., 2015; Panagiotidi et al., 2018), and strengthens the assumption that altered sensory processing – although not a core symptom according to diagnostic criteria – should be regarded as an important domain in ADHD.

If touch by others is experienced as more intense by people with ADHD, they might not enjoy social touch as much and engage in it less, as indicated by results of the self-report questionnaire in our study. Considering the importance of social-touch during development (McGline et al., 2014), tactile hypersensitivity could impact important social learning situations in early life. This might in turn lead to less social skills, and could be one of the mechanisms for the higher autistic traits and lower empathy scores observed in this ADHD sample and elsewhere (Molaholamreza Tabasi et al., 2016; Uekermann et al., 2010). Interestingly, although we found more autistic traits in participants with ADHD compared to NC, there were no associations between these traits in the ADHD group and atypical sensory processing. This replicates earlier findings (Bijlenga et al., 2017), indicating sensory dysregulation as a key feature of ADHD in adults that should be
addressed as part of the clinical assessment.

Our results in ADHD are similar to previous findings in ASD, demonstrating a lower susceptibility to the RHI and other body illusions (Cascio et al., 2012; Paton et al., 2012). It is possible that a sharper distinction between self-generated and other-generated sensations might increase the perceived boundaries of the bodily self, thereby making its perception more stable and preventing body illusions. A possible alternative could be that ADHD participants did not experience the illusion because of attention deficits during the procedure.

A sharpened boundary of the bodily self could increase somatosensory sensitivity, if it becomes harder to integrate and adapt to sensations that are not self-generated. This may explain why people with ADHD may be preoccupied with behaviorally irrelevant somatosensory stimuli – like the tag of a shirt. If such a stimulus is constantly present and cannot be habituated to, it might be hard to focus on other tasks.

In contrast to our hypothesis, ADHD participants showed intact detection threshold for tactile stimuli for all conditions. This suggest that altered central processing of somatosensory stimuli might explain the reported hypersensitivity, i.e. individuals with ADHD do not actually perceive more/weaker stimuli but rather have difficulties attenuating percepts of irrelevant stimuli. Deficits in sensorimotor gating, i.e. the suppression of response to redundant stimuli, have been reported previously, e.g. for auditory stimuli (Holstein et al., 2013), however the picture in ADHD is complicated, since other studies reported enhanced habituation (McDiarmid et al., 2017). We found stronger activity of primary somatosensory cortex in response to other-touch, however dysfunctional gating/habituation might already occur at an earlier processing step, e.g. in the spinal cord or the thalamus, which is considered to play a crucial role in sensory gating (Boehme et al., 2019; McCormick and Bal, 1994) – or the insula as we discussed above.

These findings have implications for clinical management of the reported hypersensitivity. A relationship between attention deficits and problems in attenuating irrelevant stimuli has been described in self-reports (Micoulaud-Franchi et al., 2015) and on measurements of evoked potentials in adults with ADHD (Micoulaud-Franchi et al., 2019). Sensorimotor integration training is already part of the clinical approaches to manage hypersensitivity symptoms, especially in children (Ranaschewski et al., 2001), but there are few studies on behavioral training and biofeedback, with contradictory results (Caye et al., 2019). Typical outcomes in evaluation of the efficacy of such training focuses mostly on motor skills, hyperactivity and externalizing behavior. Our results suggest an additional focus on the ability to habituate to irrelevant sensations, which might positively affect core symptoms (attention and hyperactivity). A base for novel approaches in sensorimotor integration therapy can be found in the Bayesian brain hypothesis (Friston, 2010, 2012). Within this framework, hypersensitivity might be due to heightened prediction errors, which would interfere with the attenuation of irrelevant stimuli and could lead to deficits in attention control. Based on this, a possible training could be to improve somatosensory predictions. Novel developments in brain-machine interface could also offer promising approaches, like functional electrical stimulation, which could support the learning of habituation and attention control or improve sensorimotor prediction loops (Pisotta et al., 2015).

4.1. Limitations

Participants included in the ADHD group of this study were young, adults, stable on stimulant medication, with no significant medical or psychiatric comorbidities. The high prevalence of comorbidity of adult ADHD with substance use disorder and/or ASD (Faraone et al., 2015) may limit generalizability of our findings to adults with these conditions and warrants further studies involving ADHD subjects with relevant comorbid disorders. Furthermore, we only examined people with ADHD who had not taken stimulant medication for two days. We do not know how medication may alter tactile processing and it would be interesting to compare medicated and unmedicated states in a future study.

4.2. Conclusion

We demonstrated a larger difference between self-generated and other-generated touch in the adult ADHD population. While this increased differentiation is present at the cortical level, we did not find differences at a detection threshold task, suggesting intact basic somatosensory thresholds. We furthermore show a less flexible bodily self-percept in ADHD using RHI, which might be related to the sharper self-other-distinction. Future studies need to investigate how an increased differentiation between self-generated and other-generated stimuli impacts attention, bodily self-boundaries and social cognition – and how it changes with regard to age and medication status.

5. Funding

This work was supported by grants from the Swedish Medical Research Council, Sweden (2015-02684) to HO, and from Swedish Läkarundersökning, Sweden (SLS-878101) and Lions Forskningsfond, Sweden (liu-2019-01191) to RB.

6. Disclosure

AJC has served as consultant and received speakers’ fees from Indivior, Camurus and Lundbeck, all outside the scope of this work. MH has received personal fees from BrainsWay Technologies, Indivior, and Aeliis Farma, and other income from Pfizer and Adial Pharmaceuticals, outside the scope of the submitted work. RB, MFK and HO have nothing to disclose.

CRedit authorship contribution statement

Rebecca Boehme: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Supervision, Visualization, Writing - original draft, Writing - review & editing. Morgan Frost Karlsson: Data curation, Formal analysis, Investigation, Project administration, Writing - review & editing. Markus Heilig: Conceptualization, Resources, Supervision,
and proprioceptive drift do not go hand in hand. PLoS ONE 6 (6), e21659.