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Do synaesthesia and mental imagery tap into similar cross-modal processes?

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Synaesthesia has previously been linked with imagery abilities, although an understanding of a causal role for mental imagery in broader synaesthetic experiences remains elusive. This can be partly attributed to our relatively poor understanding of imagery in sensory domains beyond vision. Investigations into the neural and behavioural underpinnings of mental imagery have nevertheless identified an important role for imagery in perception, particularly in mediating cross-modal interactions. However, the phenomenology of synaesthesia gives rise to the assumption that associated cross-modal interactions may be encapsulated and specific to synaesthesia. As such, evidence for a link between imagery and perception may not generalize to synaesthesia. Here, we present results that challenge this idea: first, we found enhanced somatosensory imagery evoked by visual stimuli of body parts in mirror-touch synaesthetes, relative to other synaesthetes or controls. Moreover, this enhanced imagery generalized to tactile object properties not directly linked to their synaesthetic associations. Second, we report evidence that concurrent experience evoked in grapheme—colour synaesthesia was sufficient to trigger visual-to-tactile correspondences that are common to all. Together, these findings show that enhanced mental imagery is a consistent hallmark of synaesthesia, and suggest the intriguing possibility that imagery may facilitate the cross-modal interactions that underpin synaesthesic experiences.

This article is part of a discussion meeting issue 'Bridging senses: novel insights from synaesthesia'.

1. Introduction

Synaesthesia has long been compared with imagery [1], owing to similarities between the phenomenological experiences [2] and that both experiences occur in the absence of an exogenous stimulus. There is compelling evidence that synaesthesia is associated with vivid mental imagery (e.g. [3,4] for reviews), particularly from studies of grapheme–colour synaesthesia [5,6] but also within other types, such as space-sequence synaesthesia ([4,7–10], although see [11]). The association between imagery abilities and synaesthesia seems to be quite nuanced, however. For example, imagery appears to be particularly enhanced within the modality that is specific to the inducer or concurrent [12], but is not constrained to the specific stimulus categories involved in the synaesthetic experience itself. Instead, enhanced visual imagery generalizes to other visual stimuli, at least in grapheme–colour synaesthetes [5].

Given that imagery affects perceptual [13,14] and memory [15] processes, and shares neural substrates underpinning perceptual function [16,17], a general enhancement of imagery abilities in synaesthetes may lead to better performance in perceptual tasks within the relevant modality. Indeed, grapheme–colour synaesthesia is associated with better colour perception [18], mirror-touch synaesthesia (MTS) with more sensitive tactile perception [19] and space-sequence synaesthesia with more efficient perception of rotated stimuli [8,9]. Studies that have formally investigated a link between imagery and synaesthesia often point to similarities between the two experiences

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regarding their effects on perception. For example, Alvarez & Robertson [20] found that when a congruent prime comprised both a real colour and induced the same synaesthetic colour, priming was enhanced in a colour naming task relative to either colour type alone. Moreover, this congruency effect correlated with synaesthetes' reported vividness of imagery, suggesting a strong connection between the two experiences. Chiou *et al.* [21] conducted a colour priming task using binocular rivalry and reported that while both a synaesthetic and imagined colour prime facilitated colour perception, a real colour prime tended to suppress colour perception when the prime and target stimulated the same monocular location. An important question therefore arises about the nature of the distinction between synaesthetic, imagined and real perceptual experiences that, according to these studies, may be influenced by the specific properties of the respective stimulation (e.g. global or local) as well as the origin of the phenomenon itself (endogenous or exogenous).

Apart from evidence that imagery is associated with synaesthesia, and that both imagery and synaesthesia show similar effects on perception, other studies have provided evidence that imagery is sufficient to mediate synaesthesia. Synaesthetic experiences themselves can be generated even when the inducing stimulus is not physically present in the environment, by being evoked through wilful imagery [6] or even by concept formation (see [22,23]). However, to date, efforts to demonstrate links between synaesthesia and mental imagery abilities have mainly been confined to the visual domain (e.g. colour or space-sequences). Indeed, Spiller *et al.* [12] reported more vivid mental imagery in synaesthetes than non-synaesthetes when the sensory modality of the inducer and concurrent was congruent. Thus, when both the inducer and concurrent are visual, it might be possible that imagery is enhanced owing to repeated stimulation within the visual system. What is less clear is whether imagery would also consistently be enhanced across modalities when the synaesthetic concurrent arises in a sensory modality that differs from that of the inducing stimulus [12]. The nature and vividness of imagery in incidences of synaesthesia that are triggered across modalities, and in modalities other than vision, have rarely been investigated.

In typical perceptual processing, imagery can influence multisensory perception (e.g. [24,25]). For example, Berger & Ehrsson [26] reported that imagined sounds can trigger similar cross-modal illusions to their real counterparts, including the ventriloquist effect and McGurk illusion. Furthermore, Lacey *et al.* [27] argued for a central role of imagery in the interactions underpinning the cross-modal perception of objects. It is therefore possible that imagery abilities in synaesthesia may be linked to the cross-modal interactions underpinning the experience and that, moreover, synaesthesia (like imagery) may affect cross-modal interactions that are commonly experienced by all.

One intriguing aspect of synaesthetic experiences is that there appears to be little evidence that the concurrent affects the perception of stimuli beyond the specific synaesthetic association itself. In other words, there is evidence to suggest that colour concurrents can enhance or interfere with colour perception (e.g. [28,29]), and demonstrations of bidirectionality in synaesthetic associations suggest that colour concurrents can even affect the perception of the associated trigger stimulus (e.g. [30]). However, consistent evidence for a more generalized benefit of synaesthesia on multisensory perception has not been forthcoming (see [31,32] for a discussion). This is somewhat unexpected, given the evidence for broad-range differences in patterns of cortical connectivity and functional activation between synaesthetes and non-synaesthetes ([33,34] but see [35]), including activation differences in early visual regions of the brain [36]. Furthermore, given that synaesthesia is considered a 'mixing of the senses' and involves multisensory processing of the inducing stimulus [37], the specificity of the effect of the synaesthetic experience on associated perceptual processes is surprising. However, one possible reason for our lack of knowledge is that the role of imagery in mediating cross-modal processes has not been fully considered in investigations of synaesthesia. Here, we conducted two experiments to assess whether synaesthesia is associated with enhanced imagery abilities and whether this has an impact on cross-modal perception.

2. Experiment 1: self-reported imagery in mirror-touch synaesthetes

Mirror-touch synaesthesia provides a candidate model of cross-modal synaesthesia for investigating these effects: in MTS, the concurrent is experienced in a sensory modality (touch) that differs from that of the inducing stimulus (vision). An individual with MTS automatically and consistently experiences a physical sensation of touch on their own body when viewing touch on another's body [38,39]. MTS has a reported prevalence of approximately 1.6% [38] in the general population, and is associated with more typical processes underpinning social perception, including empathy [40]. The unique combination of activation within mirror neuron systems in the brain, which typically function to represent another person's actions as one's own [41,42], as well as multisensory regions governing the sense of self, indicates that atypical self-processing and self–other distinctions are present in MT synaesthetes [39].

We tested self-reported imagery in a group of MT synaesthetes and compared their performance to two different groups: a synaesthete group who did not have MTS and a non-synaesthetic control group. Following an initial screening phase, imagery in the tactile domain was tested across two different tasks: somatosensory imagery (ratings of sensitivity across the body) and tactile imagery (of object properties) in all participants.

(a) Methods

(i) Participants

Thirty participants volunteered to take part in this study and were recruited from a large sample of individuals ($N = 366$, described in [43]) who attended a public exhibition at the Science Gallery Dublin. All participants were fluent English speakers and 66% (20/30) reported English as their native language. Based on our screening procedure (described in 2a(ii)), 10 individuals were identified as MT synaesthetes (MTS), 10 as having other forms of synaesthesia (non-MTS) and 10 as having no synaesthete experiences (control). Both the non-MTS and control groups were age and sex matched to the MTS group, and selected via stratified random sampling from larger samples of qualifying participants. Demographic details of all three groups of participants are provided in table 1.

Table 1. Demographic information of the three groups (MTS, non-MTS and control) tested in experiment 1.

	MTS *N* = 10 (%)	non-MTS *N* = 10 (%)	control *N* = 10 (%)
sex			
female	6 (60)	6 (60)	6 (60)
male	4 (40)	4 (40)	4 (40)
age			
13–17	3 (30)	3 (30)	3 (30)
18–35	4 (40)	4 (40)	4 (40)
36–55	2 (20)	2 (20)	2 (20)
56+	1 (10)	1 (10)	1 (10)
handedness			
right-handed	7 (70)	9 (90)	8 (80)
left-handed/ambidexterous	1 (10)/2 (20)	1 (10)	1 (10)/1 (10)
nationality			
European	6 (60)	9 (90)	8 (80)
North American	3 (30)	0	2 (20)
Asian	1 (10)	1 (10)	0
diagnosis of neurological disorder			
no	9 (90)	10 (100)	10 (100)
MT synaesthesia ratings (1–7)			
mean frequency of MTS	5.7	3	2.4
mean strength of MTS to others			
familiar	5.71	3.8	2.6
unfamiliar	4.29	2.1	1.8
additional types of synaesthesia (frequency of 'yes' response)			
none	1 (10)	0	10 (100)
grapheme–colour	2 (20)	2 (20)	0
music–colour	3 (30)	4 (40)	0
taste–colour	1 (10)	2 (20)	0
other (not listed)	3 (30)	2 (20)	0
ratings to MT videos (1–7)			
mean sensitivity (s.d.)	5.30 (1.26)	2.54 (1.57)	2.45 (1.72)
range	4.96–5.79	1–4.92	1–4.54
body location mean sensitivity (s.d.)			
back of neck	5.85 (1.27)	2.55 (1.55)	2.78 (2.04)
ear	5.12 (1.29)	2.77 (1.70)	2.58 (1.73)
hand (ego)	4.95 (1.19)	2.55 (1.64)	1.85 (1.09)
hand (allo)	5.63 (1.19)	2.77 (1.73)	2.52 (1.82)
mean sensitivity to stimulus type (s.d.)			
real hand	5.46 (1.22)	2.71 (1.70)	2.35 (1.68)
fake hand	5.04 (1.31)	2.51 (1.53)	2.45 (1.68)
paintbrush	5.40 (1.23)	2.40 (1.48)	2.55 (1.80)

(ii) Materials and apparatus

A general questionnaire was designed to determine basic demographic details of the participants (e.g. sex, age, nationality) as shown in table 1. The main study comprised three different sessions; a screening phase, somatosensory mental imagery (SMI) and tactile mental imagery (TMI) tasks. These two main tasks were conducted in a testing booth, measuring 2 m by 2 m, and surrounded by a black curtain that was closed during testing. The booth was positioned within a quiet section of the exhibition area of the Science Gallery. The entire experiment was presented on a computer (Dell Optiplex 790) with the monitor (1920 × 1080 pixel resolution with a refresh rate of 60 Hz) resting on a table and positioned approximately 70 cm from the seated participant. All experimental tasks were programmed using PsychoPy [44].

The screening phase involved both a questionnaire and rating study. The questionnaire included two questions relating to MTS specifically, and one question on other forms of synaesthesia. The MTS questions related to how frequently the participant experiences a sensation of touch on their own body when viewing touch on another person's body in everyday life (from 1 *never* to 7 *all the time*) and the strength of tactile 'mirroring' when viewing touch on the body of a personally familiar or unfamiliar individual (from 1 *very weak* to 7 *very strong sensation*). Finally, participants were provided with a brief description of synaesthesia (*Synaesthesia is described as a curious mingling of the senses. For example, some people see colour or experience taste when they hear sounds*) and were asked to indicate if they always experience colour to any of the following stimuli: (i) letters and/or numbers (i.e. indicating grapheme–colour synaesthesia), (ii) music (auditory–colour synaesthesia), (iii) while eating (gustatory–colour synaesthesia), or if they experienced (iv) another form of synaesthesia not listed. Participants were also asked to confirm (v) if they had synaesthesia. Participants provided 'yes' or 'no' confirmatory responses only to the general questions on synaesthesia.

For the rating study of the screening phase, the stimulus set comprised short video clips of one of two different models, a male and a female, being stroked on either their right hand (dorsal), their right ear or back of the neck. The hand was presented twice, in separate video clips, from an allocentric and egocentric perspective. Each body location was shown stroked three times per video clip, once each with a different stimulus inducer of either another person's real hand (opposite sex to the actor), a fake hand or a paintbrush. The experimenter's hand controlling the fake hand or paintbrush was not visible during the video. The direction and velocity of the stroking were matched across videos to an approximate stroking speed of $8\,\mathrm{cm\,s^{-1}}$. A total of 24 video clips (two actors, four body sites and three stimulus inducers) comprised the set of stimuli for the screening phase. Each video clip lasted no longer than 6 s and participants were presented with instructions to provide a rating response after viewing each clip.

For the SMI test, the stimulus set comprised schematic illustrations of individual body parts with specific anatomical regions highlighted in colour (for examples of these stimuli, see electronic supplementary material). The total number of 21 stimuli consisted of the following body sites: hallux, ball of the foot, foot underside, dorsal foot, the shin, thigh, abdomen, chest, neck, mouth, nose, cheek, ears, forehead, upper arm, forearm, dorsal hand, palm of the hand, dorsal finger, finger underside and the fingertips. Each stimulus was displayed for 2 s and participants were then presented with instructions to provide a rating response.

The stimuli for the TMI test consisted of the names of five objects; bubble wrap, ice cube, sandpaper, velvet and wet sponge. Each object name was presented at the top of the screen along with a specific instruction to rate the object on each of its properties (for an example of the stimulus display, see electronic supplementary material). These properties included surface force (e.g. required to pop the bubble wrap, to feel the ice or sandpaper etc.), resistance (hard or soft), texture (rough or smooth) and object weight (light or heavy). Each object name stimulus in this task was presented until the participant provided a rating response.

(iii) Design and procedure

Before entering the testing booth, participants were first invited to take part in the study by providing informed, written consent and basic demographic information at a sign-in station. The parent or guardian of any individual under the age of 18 was required to complete the consent form before the individual could participate in the study. The demographic details of all participants are provided in table 1. Each participant was then escorted to the testing booth, where they were presented with the series of three rating tasks; the screening test for MTS, TMI and SMI tasks. Trials were randomly presented across participants for each of the imagery tasks. A practice trial was first provided that required the participant to rate the taste of a lemon (from 1 *very sweet* to 7 *very bitter*) using the same rating scale as in the other tasks. The screening test trials appeared immediately after this initial practice trial. Each video clip in a trial was preceded by a short, 3 s prompt that asked *How much do you feel this touch on your own body?* to which participants responded on a rating scale from 1 (*I felt no touch*) to 7 (*I felt the touch very strongly*).

For the TMI rating task, participants were instructed to imagine feeling various object materials (bubble wrap, ice cube, sandpaper, velvet, wet sponge) with their eyes open and to provide imagery ratings for each material (see electronic supplementary material for further details). Specifically, for each material, participants were required to indicate the vividness of their tactile imagery for all of the following object properties: force, resistance, texture and weight, using a Likert rating scale. Brief explanations were provided for these tactile properties, for example, participants were asked to imagine the force needed to pop the bubble wrap, imagine squeezing the wet sponge or imagine feeling the resistance (i.e. the hardness or softness) of a material. They were encouraged to provide ratings of their imagery ranging from 1 (*I cannot imagine this*) to 7 (*I can vividly imagine this*).

For the SMI rating task, participants were asked to refer to each schematic illustration of the body shown in each trial, and imagine being stimulated on their own corresponding body site by a light brushstroke. They then provided a rating of their sensitivity using a Likert scale ranging from 1 (*not sensitive at all*) to 7 (*extremely sensitive*).

To respond (in all rating tasks), the participant used a mouse to move a triangular marker along a scale until it reached the point on the scale corresponding to their rating. They then clicked the mouse to confirm their rating. The default position of the marker was always the midpoint of the scale and participants were encouraged to use the whole scale.

The final sequence of testing involved a series of questions that acted as a further screening test for synaesthesia, including two questions on MTS to which the participant provided a rating response, and five on other types of synaesthesia (or none), as described earlier. The entire experiment lasted no longer than 10 min per participant.

(iv) Data analysis

The analyses were performed using R (v. 3.5.0; [45]) on R studio [46]. The ANOVAs were conducted using the ez package [47] and type 3 sum-of-squares to test for significant main effects and interactions. Participants' mean Likert ratings to the screening, TMI and SMI tasks were entered into mixed-design ANOVAs for statistical analysis. Where appropriate, the Greenhouse–Geisser correction was applied to adjust the degrees of freedom of within-subject tests to correct for violations of the sphericity assumption and, in these cases, the adjusted p-value is reported. Separate *post hoc* tests were carried out for significant main effects or interactions (one-sample t-test for within-subject and Tukey HSD for between-subject comparisons). When multiple one-sample t-tests were performed, the Bonferroni correction was used to maintain a family-wise Type 1 error rate at 0.05 and the adjusted p-value is reported.

(v) 'MT' synaesthetes, 'non-MT' synaesthetes and 'control' group selection

The synaesthete participants were identified from their responses to the combined screening tests, that is, based on their self-reported answers to the series of questions on MTS and other types of synaesthesia, as well as their rating scores to the video clips designed to evoke MTS. We used two main, co-occurring inclusion criteria for MTS. First, we decided that, for each participant, the minimum cut-off rating in response to the mirror-touch videos was 5 (i.e. corresponding to a strong tactile sensation when viewing the videos) and the reported frequency of tactile 'mirroring' experienced in everyday life should be higher than a rating of 4 (corresponding to 'a lot of the time'). Based on the overall mean rating scores in response to the video clips alone, 12 candidates (3.3% of the total sample) qualified for consideration. Of these, three failed to meet our inclusion criterion of frequently experiencing mirror-touch (all three reported 'never' to whether they experienced a sensation of touch on their own body when viewing touch on other bodies in everyday life). We decided that an additional participant with a mean score of 4.96 in response to the video clips that was slightly lower than criterion, but who reported frequently experiencing MTS qualified for inclusion, yielding a total sample of 10 (MTS group, table 1). This final sample of MT synaesthetes represents a prevalence rate of 2.7% from the larger sample, which is equivalent to, albeit slightly higher than, previous estimates of between 1.6 and 2.5% [37]. We also tested for the presence of co-occurring synaesthetic experiences in these and other participants. Nine participants from this MTS group also reported experiencing another form of synaesthesia. All reported no history of physical impairment but one reported a history of neurological impairment (which we deemed as transient and unrelated to their synaesthesia).

The participants allocated to the MTS group provided a mean rating of 5.70 (±0.95) on the frequency of tactile mirroring experienced in everyday life. Of these participants, seven provided mean ratings of 5.71 (±0 0.95) and 4.29 (±2.06) in response to familiar and unfamiliar individuals, respectively, which did not differ statistically [$t_6 = 1.70$, $p = 0.14$] (three MT synaesthete participants did not provide a response to this question). We found no evidence that the ratings to the different body sites or stimulus types differed for this group (see 'ratings to MT videos' in table 1).

Participants were allocated to the 'Non-MTS' group or the 'control' group based on their responses to the questionnaire (i.e. whether they reported experiencing synaesthesia or not) and on providing lower ratings to the video clips than the cut-offs mentioned earlier. Of the total number of synaesthetes identified through self-report ($N = 165$), 10 were selected through stratified random sampling, with the constraints that they were age- and sex-matched to the MTS group and had no history of neurological or physical impairments. The final sample included two grapheme–colour, four auditory–colour, two gustatory–colour and two reporting 'other' types of synaesthesia. Finally, 10 participants who self-reported experiencing no form of synaesthesia were selected through stratified random sampling and assigned to the control group. Again, these participants were matched to the MTS group and reported no history of neurological or physical impairment. All ratings provided by each of these groups to the screening test (video clips) were significantly lower than those provided by the MTS group, as expected with our procedure ($F_{2,27} = 20.4$, $p < 0.001$, $\eta^2_{\text{gen}} = 0.5$). We also found a significant main effect of body location on the ratings ($F_{2,54} = 4.96$, $p = 0.015$, $\eta^2_{\text{gen}} = 0.02$), which was driven by higher ratings to the neck area than other body sites. No other differences or interactions were found. Further details of this analysis across groups and body location are provided in electronic supplementary material.

(b) Results

The mean ratings provided by each of the MTS, non-MTS and control groups to each of the TMI and SMI tasks are shown in figure 1. We first compared the groups' ratings to the TMI task. A mixed-model 3 (group) × 4 (object property) × 5 (material) ANOVA was performed on participants' mean ratings. A main effect of group was found ($F_{2,27} = 4.86$, $p < 0.01$, $\eta^2_{\text{gen}} = 0.15$). A *post hoc* Tukey HSD test revealed that the MTS group provided significantly higher TMI ratings (M = 5.93 ± 1.56) than the non-MTS (M = 4.72 ± 1.85; $p < 0.001$) and control (M = 4.25 ± 1.94; $p < 0.001$) groups, and the non-MTS group provided higher ratings than the control group ($p < 0.02$) (figure 1*a*).

There were also significant main effects of material ($F_{4,108} = 2.59$, $p < 0.041$, $\eta^2_{\text{gen}} = 0.02$) and object property ($F_{3,81} = 14.49$, $p < 0.001$, $\eta^2_{\text{gen}} = 0.04$), which were qualified by a significant interaction between these factors ($F_{12,324} = 6.54$, $p < 0.001$, $\eta^2_{\text{gen}} = 0.05$) as shown in figure 2. *Post hoc* pairwise comparisons, with Bonferroni correction, revealed differences between object properties to the sandpaper material only, with higher ratings to texture than force, lower ratings to weight than either texture or resistance and lower ratings to force than resistance (see electronic supplementary material, figure S1 for an illustration of these comparisons). Differences between material type were also found to be dependent on object properties but were mainly owing to higher ratings on force and weight given to sandpaper than to the wet sponge or bubble wrap. The effect of group did not interact with any of the other factors.

The groups' mean ratings to the somatosensory imagery (SMI) task are shown in figure 1*b*, and mean ratings provided by each group to each body sight are provided in figure 3. To simplify the analysis, the 21 body parts were clustered into five main body regions as follows: head (mouth, nose, cheek, ears, forehead), upper body (abdomen, chest, neck, upper arm, forearm), lower body (shin, thigh), foot (hallux, dorsal foot, foot underside, ball of foot) and hand (dorsal

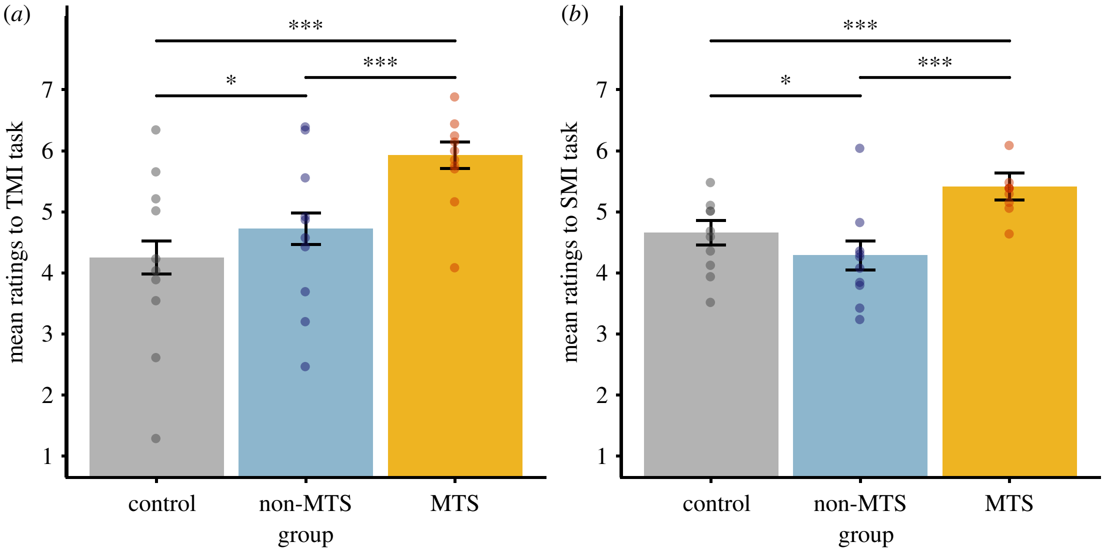

Figure 1. The mean ratings provided to the (*a*) TMI and (*b*) SMI tasks by each of the control, non-MTS (non-MTS) and MT synaesthesia (MTS) groups in experiment 1. Individual participant mean ratings are also shown (as filled circles) within each group. Error bars represent 95% confidence intervals. (Online version in colour.)

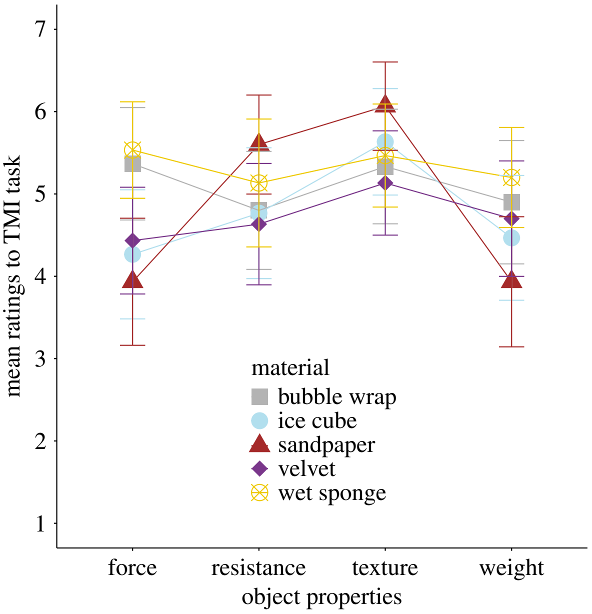

Figure 2. Plot showing the interaction between ratings provided to materials and object properties found in experiment 1. Error bars represent 95% confidence intervals. (Online version in colour.)

hand, palm of the hand, dorsal finger, finger underside, fingertip). A mixed-model 3 (group) × 5 (body region) ANOVA was then conducted on participants' mean ratings to imagined sensitivity to a tactile stimulus on each viewed body site. A main effect of group was found ($F_{2,27} = 7.92$, $p < 0.01$, $\eta^2_{\text{gen}} = 0.18$) and a *post hoc* Tukey HSD test confirmed significantly higher ratings by the MTS group ($M = 5.41 \pm 1.61$) than either the non-MTS ($M = 4.29 \pm 1.72$) or control ($M = 4.66 \pm 1.48$) groups ($ps < 0.001$), and lower ratings by the non-MTS than control group ($p = 0.047$). A main effect of body region was also found ($F_{4,108} = 3.35$, $p < 0.02$, $\eta^2_{\text{gen}} = 0.07$). *Post hoc* pairwise comparisons with Bonferroni correction confirmed higher ratings to the head region ($M = 5.16 \pm 0.87$) than the hand ($M = 4.59 \pm 1.04$; $p < 0.001$) and foot ($M = 4.45 \pm 1.16$; $p = 0.02$) regions. There was no evidence for an interaction between group and body region ($p > 0.05$).

(c) Discussion

Our results support the idea that synaesthesia is associated with enhanced imagery within the sensory domain of the synaesthetic experience [12], and provide evidence for cross-modal, visual to somatosensory imagery abilities. First, we found higher ratings of imagined touch in mirror-touch synaesthetes than in other synaesthetes or non-synaesthete controls when viewing regions of the body. This finding is not that surprising, given that mirrored somatosensory sensitivity when viewing tactile stimulation of another person is central to the reported experiences of MT synaesthetes [48], as well as reports of better tactile perception in this group [19]. Interestingly, the ratings of individuals with other reported forms of synaesthesia, so-called non-MT synaesthetes (mainly synaesthesia within visual and auditory modalities) were lower in the SMI test than those provided by the control group. This result is consistent with other reports of deactivated or negative neural responses in synaesthesia [34] and in imagery [49]. The difference between non-MTS and control groups was marginal, however, and future studies may help to establish the veracity of this finding.

Our second finding, that MTS is associated with enhanced tactile imagery of object properties and materials that are not directly implicated in the synaesthetic experience itself, extends previous findings of enhanced imagery to within-modal stimuli beyond those experienced in synaesthesia [5,12]. Moreover, non-MTS synaesthetes also reported enhanced imagery to these object stimuli relative to controls, suggesting a role for either multiple types of synaesthesia [12] or the involvement of vision in synaesthetic subtypes on enhanced tactile imagery. Indeed, we found it somewhat surprising that enhanced imagery for touch would extend to visual descriptions of distal objects and their properties in MTS in particular, given that such a task is more related to haptic perception than somatosensation *per se* [50]. However, touch can activate visual brain regions underpinning object perception (i.e. the lateral occipital complex, see [51]); therefore, this finding may reveal the multisensory neural architecture supporting the representations of objects.

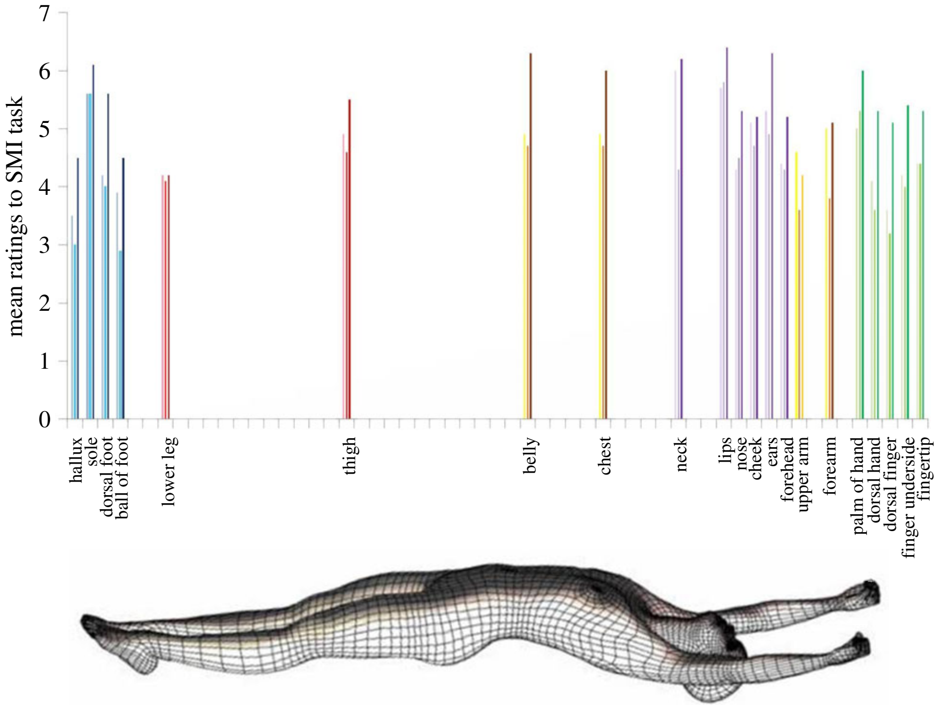

Figure 3. Participants mean ratings to the SMI task for each of the control, non-MTS and MTS groups (adapted from [48]). Groups are colour coded in different shades as follows: control (light), non-MTS (intermediate) and MTS (dark). The five main body regions are colour coded as follows: head (purple), upper body (yellow–orange), lower body (red), foot (blue) and hand (green). (Online version in colour.)

An important limitation to our study is that self-reported synaesthetes were not subjected to consistency testing, which is often considered a hallmark of genuine synaesthesia [52]. We were constrained on the testing time available within the large public exhibition. Nevertheless, we are confident that our combined procedures helped us correctly identify individuals with MTS. Other types of synaesthetes were identified by questionnaire only, which we recognize as being less than ideal. Indeed, the prevalence of synaesthesia in our total sample was rather high (45% self-reported as synaesthetes) compared to previous estimates. This may have occurred if synaesthetes were particularly drawn to a public exhibition entitled ‘Fake’, which was advertised as also including tests of perception. However, other results assure us that these cases are also genuine. First, the prevalence rates from our sample are consistent with the literature in that more synaesthetes identified as having grapheme–colour synaesthesia than other forms [5,53] and MTS was a relatively rare form of synaesthesia [54]. Second, the reported main effects did not change when we repeated the stratified, random-sampling approach on the non-MTS and control groups.

3. Experiment 2: cross-modal correspondences from the synaesthetic colours

The results of experiment 1 suggest that synaesthesia is associated with imagery within the tactile domain that is triggered by a stimulus in another modality (vision). Unlike other cross-modal associations that are common to all [55], and influenced by associations found in the natural environment (e.g. [56]), it is assumed that synaesthetic experiences are resistant to learning. In other words, although the specific synaesthetic associations may initially arise through learning (e.g. [57,58]), once the concurrent is established, the specific synaesthetic association with the inducer persists despite repeated evidence to the contrary from the environment (cf. changes owing to ageing [59]; or pharmacological intervention [60]).

However, the assumption that synaesthetic experiences are encapsulated is not consistent with evidence that synaesthesia can affect perception, recall or even enhanced cross-modal imagery reported earlier. It remains possible, therefore, that the synaesthetic concurrent can, in itself, tap into other forms of information processing, although evidence for such influences beyond the synaesthetic association (e.g. letters and colours in grapheme colour synaesthesia) remains elusive. Nevertheless, such evidence might help provide insight into the mechanisms supporting the general enhancements associated with synaesthesia. Here, we investigated the extent to which synaesthetic experiences, or concurrents, are encapsulated using a method that exploits cross-modal correspondences. We were particularly interested in investigating whether synaesthesia influences multisensory or cross-modal processes, since these reflect more typical perceptual tasks in the natural environment, as well as neural processing in the brain [61]. Specifically, we tested whether cross-modal, tactile correspondences were also associated with synaesthetic experiences in the visual domain. To that end, we adapted a task described by Pinkerton & Humphrey [62], which was designed to test whether different colours are associated with differences in the tactile property of weight [63].

(a) Methods

(i) Participants

Sixteen grapheme–colour synaesthetes (12 female, mean age: 21.53 years old) and 22 age-matched controls (16 female, mean age: 22.1 years old) with normal or corrected-to-normal vision volunteered to take part in the study. Participants were recruited from the student population of Trinity College Dublin and were compensated with research credits for their

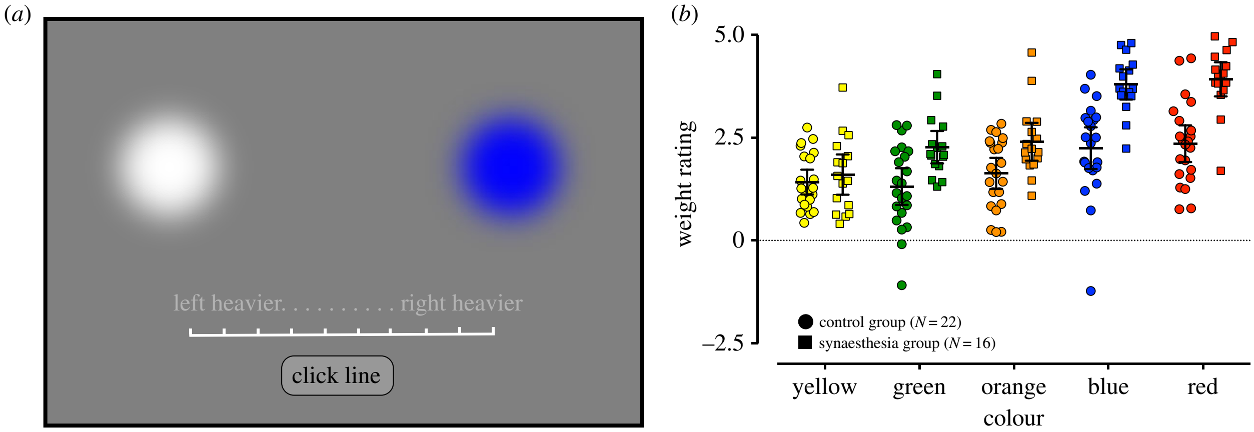

Figure 4. (*a*) Example of a stimulus in the colour patch test used in experiment 2. (*b*) Mean weight ratings provided across both groups of participants to colour patches. Positive (negative) weight ratings indicate that the test stimulus was judged to be heavier (lighter) than the standard stimulus. The dotted line indicates when both stimuli were considered equal in weight. Error bars represent 95% confidence intervals. (Online version in colour.)

time. All participants were naive to the purposes of the study and gave their informed, written consent prior to their inclusion.

All participants in the synaesthesia group reported seeing colours in response to letter and digit stimuli. Synaesthesia was verified using the Synaesthesia Test Battery [64] and a customized test of consistency matching over time (see §3a(iii)). Participants with a score of less than 0.9 on the test battery and a test–retest consistency of 80% over a period of at least one week on the customized test were included in the synaesthesia group. Participants who failed to meet either of these criteria were excluded from the study. Control participants also performed both tests to rule out the possibility that they were subject to synaesthetic experiences.

(ii) Stimuli

Stimuli consisted of circular colour patches and uppercase letters presented on a grey background. Patch stimuli were masked by a Gaussian luminance profile with a fixed standard deviation of 1.32° and could take one of six isoluminant colours (red, blue, green, orange, yellow, white) with an average luminance of $13\,\mathrm{cd\,m^{-2}}$. Letter stimuli were presented in Times New Roman font and were 8° of visual angle in height from a viewing distance of 57 cm. Fifteen letter stimuli were used in total, all of which were white. Stimuli were displayed on a gamma-corrected BenQ XL2410T LCD monitor at a resolution of 1280 × 1024 pixels at a refresh rate of 120 Hz. The maximum luminances available for red, green and blue were 56, 178 and $13\,\mathrm{cd\,m^{-2}}$, respectively. All stimuli were created and all data were collected using PsychoPy [44,65].

(iii) Procedure

Participants performed a weight-matching task with colour patch and letter stimuli in separate blocks, the order of which was counter-balanced across participants. In both blocks, participants were presented with two stimuli located 8° either side of the centre of the screen and a rating scale located below the stimuli (figure 4*a*). Participants were instructed to imagine that the mouse cursor was an adjustable fulcrum and to position it at the point on the rating scale at which they judged the two stimuli to be balanced in weight. There was no time limit on responses and once the participant was satisfied with their answer, they clicked an ‘Accept’ button. Prior to the experiment, participants completed a short practice block to familiarize them with the task.

Each participant completed a total of 200 weight-matching judgements (100 trials with colour patch and 100 trials with letter stimuli). In the colour patch block, the white stimulus acted as the standard stimulus and was present for all trials. The test stimulus was selected at random on each trial from the remaining colours, with each test colour being displayed 20 times. The positions of the standard and test stimuli were randomized on each trial, such that there was an equal probability that the standard stimulus would appear on the left or right of the screen. The procedure for the colour patch block was identical for the synaesthesia and control groups.

The letter stimuli were determined from a customized test administered to the synaesthesia group prior to the experiment in which participants provided a detailed description of the colour induced by each letter. The test was repeated two weeks later to ensure retest consistency of 80% or above. To select appropriate letter stimuli for each participant, letter descriptions that included any of the colours used in colour patch block were initially identified as potential stimuli for the letter block and, where possible, letters were retained when the induced colour was also described as ‘strong’ or ‘saturated’. To select a standard stimulus for each participant, preference was given to letters that either did not induce a colour or induced the colour white. This letter selection process led to a unique set of letters for each synaesthete, with 15 distinct letters used across all 10 participants. For each participant in the control group, five test letters were selected at random from the 10 most frequently selected letters in the synaesthesia group, while the standard letter was always the letter ‘O’. All other aspects of the experimental procedure were identical to the colour patch block.

(iv) Data analysis

Individual weight judgements were converted to a numeric value between 5 and −5, where positive/negative values indicated that the test stimulus was judged to be heavier/lighter than the standard. Each test stimulus was presented 20 times in a block and the mean of these weight judgements was taken as the weight rating for that stimulus. These values were subsequently group-averaged for statistical analysis,

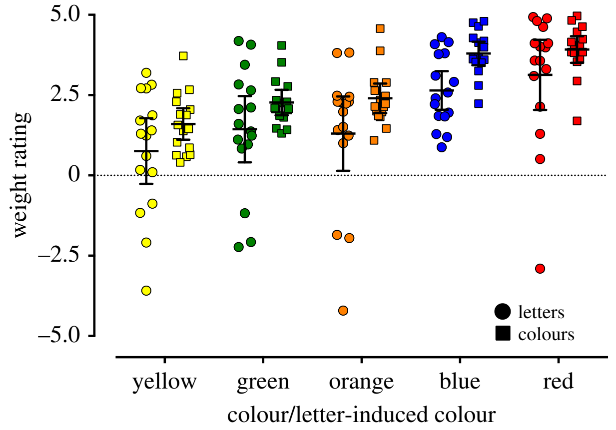

Figure 5. 'Weight' responses in synaesthete group to letters and colour patches. Error bars represent 95% confidence intervals. Positive (negative) weight ratings indicate that the test stimulus was judged to be heavier (lighter) than the standard stimulus. The dotted line indicates when both stimuli were considered equal in weight.

where within- and between-group comparisons were made using different types of ANOVA. Where appropriate, the Greenhouse–Geisser correction was applied to adjust the degrees of freedom of within-subject tests to correct for violations of the sphericity assumption and, in these cases, the adjusted p-value is reported. When multiple one-sample t-tests were performed, the Bonferroni correction was used to maintain a family-wise Type 1 error rate at 0.05 and the adjusted p-value is reported. All statistical analyses were performed in GraphPad Prism 6.0, with type 3 sum-of-squares used to test for significant main effects and interactions.

(b) Results

The group-averaged results for the synaesthesia group and the age-matched controls to the colour patches are shown in figure 4*b*. For both groups, all colours tested were judged to be heavier than the standard white stimulus, as indicated by the positive weight ratings for every test colour. Furthermore, the magnitude of the weight rating varied for different colours, with a similar ranking of weights observed across both groups. A one-way repeated-measures ANOVA confirmed that the magnitude of weight judgements varied for different colours in both the control group ($F_{3,74} = 38.18$, $p_{\text{adj}} < 0.001$, $\eta^2 = 0.45$) and the synaesthesia group ($F_{3,49} = 35.76$, $p_{\text{adj}} < 0.001$, $\eta^2 = 0.58$), while one-sample t-tests against a weight rating of 0 determined that all colour patches were significantly heavier than the white stimulus (control group: ($ts_{21} > 6.12$, $p_{\text{adj}} < 0.001$), synaesthesia group: ($ts_{15} > 6.97$, $p_{\text{adj}} < 0.001$)). Finally, a mixed-model 2 (group) × 5 (colour) ANOVA revealed that there was a significant main effect of group on weight ratings ($F_{1,36} =$, $p < 0.001$, $\eta^2 = 0.17$), with synaesthetes ranking the colours as heavier overall.

We then examined whether the colours experienced by grapheme–colour synaesthetes in response to letters also have an apparent weight. To facilitate comparison with the colour patch data, we averaged across these different letter–colour combinations, such that the data in figure 5 are expressed in terms of the weight responses to the colour patches (colour) and to the colour induced by the letter stimuli (hereafter referred to as 'letter-induced colours'). As with the colour patch data, all of the letter-induced colours were rated as heavier than the standard stimulus, as indicated by the positive weight rating values shown in figure 5. Furthermore, there was a striking resemblance in the ranking and the relative magnitudes of weight ratings for both datasets, with red and blue again being ranked as the heaviest and yellow as the lightest. A one-way repeated-measures ANOVA confirmed that the magnitude of weight ratings varied for the different induced colours ($F_{3,43} = 16.54$, $p_{\text{adj}} < 0.001$, $\eta^2 = 0.3$), although subsequent one-sample t-tests revealed that only the red, blue and green conditions were significantly different from a weight rating of 0 (red: $t_{15} = 6.17$, $p_{\text{adj}} < 0.001$, Cohen's $d = 1.55$; blue: $t_{15} = 9.38$, $p_{\text{adj}} < 0.001$, Cohen's $d = 2.34$; green: $t_{15} = 2.97$, $p_{\text{adj}} < 0.05$, Cohen's $d = 0.74$). The weight rating responses to the colour patch stimuli were significantly higher than those to the letter stimuli ($F_{1,30} = 4.887$, $p = 0.035$, $\eta^2 = 0.076$). We also conducted a correlation analyses that revealed a strong positive correlation between the weight ratings for the two types of stimuli in the synaesthete group ($R^2 = 0.372$, $p < 0.001$), while the slope of the best fitting regression line to the data was significantly different from 0 ($a = 0.361$, $p < 0.001$). Moreover, fitting individual regression lines to each participant's data confirmed that there was a positive slope for all 16 datasets (ranging between 0.22 and 1.67), suggesting that this relationship was robust to the level of individual participants. Crucially, we found no consistent pattern in the weight ratings assigned to different letters by the control group and a one-sample t-test confirmed that overall these ratings were not significantly different from a weight rating of 0 ($t_{109} = 0.9466$, $p = 0.35$, Cohen's $d = 0.09$).

(c) Discussion

First, our results based on real colour patches replicated those previously reported [62]: red and blue were consistently perceived as the heaviest colours, and yellow as the lightest. Moreover, our findings provide an important extension: here, we found that induced, synaesthetic colours are sufficient to evoke cross-modal correspondences of weight, typically considered a tactile property of objects, and do so in a manner that is akin to the correspondences experienced with veridical colours. For grapheme–colour synaesthetes, letters that induced the colour red, or blue, were perceived as 'heaviest' while letters that induced the colour yellow were perceived as lighter. This finding challenges the idea that the effect of the synaesthetic concurrent on perception is specific to its domain (e.g. colour [18]; or somatosensation [19]), or that of the inducer [30]. By contrast, our results provide evidence for the perceptual reality of the synaesthetic concurrent, particularly its role in cross-modal interactions that are commonly experienced.

4. General discussion

Our results add to growing evidence that synaesthesia is linked to more vivid imagery, and that imagery abilities generalize to stimuli not directly involved in the synaesthetic experience [5,12]. Furthermore, we provide evidence that MTS is associated with heightened cross-modal imagery: visual stimuli evoke proximal tactile sensations on the body as well as enhanced tactile imagery of distal, external objects. A distinction between passive (somatosensation) and active (haptics) touch has previously been reported within the tactile system [66]; therefore, these results are interesting in that they show generalization of imagery abilities beyond the limits of the synaesthetic interactions themselves as well as the functional organization of the somatosensory system.

We also report a novel finding that a visual synaesthetic concurrent can mediate cross-modal interactions. The results of our second experiment show that a tactile feature, weight, can be readily associated with an induced colour in a manner that is similar to viewing the real colour. Thus, correspondences were generated in a modality beyond vision that is not typically associated with grapheme–colour synaesthesia. Furthermore, the nature of the cross-modal correspondences were not unique to the grapheme–colour synaesthetes. Taken together, our findings challenge the idea that the synaesthetic concurrent is entirely encapsulated. Specifically, synaesthesia is associated with a general ability to imagine other stimuli within the same modality, as well as influencing perceptual associations in other modalities. It is unclear, therefore, why the synaesthetic concurrent appears to resist other cognitive influences and, despite the evidence that it is associated with individual differences in imagery and perception, appears to coexist with these other experiences without the representation of the synaesthetic concurrent being affected.

Although our study does not directly address the issue of causality, there may be more to the ‘suspicious coincidence’ that enhanced imagery is found in synaesthetes. For example, it may be that both synaesthesia [5,67] and vivid imagery [16,68] arise from higher baseline excitability within sensory cortices than in the general population. The cortical responses in S1 and SII in MT synaesthetes are particularly intriguing, first because they arise in response to visual depictions of tactile stimulation on another’s body and second, the responses are specific to viewing real bodies being touched as opposed to objects or fake bodies [14]. Moreover, hyper-excitability of S1, induced by neuro-stimulation, produces MT phenomena [3,4], and (pre-) viewing another person’s body region modifies tactile sensitivity on one’s own body [69] in non-synaesthetic populations. These findings suggest that similar cross-modal connections are present in all, synaesthete and non-synaesthete alike.

Our results also raise the question of what is the nature of the representations at the interface between imagery, synaesethesia and perception. Clearly, there are important phenomenological differences between synaesthesia and imagery, as well as the fact that imagery is more widely experienced. Previous studies suggest that any differences found between perception, imagery and synaesthesia may reflect different stages of information processing along the sensory pathways. For example, Arnold *et al*. [70] reported that the variability in responses to synaesthetic colour matching was similar to colour matching from memory, but larger than to real colour matching, suggesting that synaesthetic colours are akin to colour memory than perception and that synaesthetic colours likely arise at a higher level of analysis in the brain [71]. Indeed, these psychophysical findings are consistent with neuroimaging reports demonstrating activation in higher areas of the brain to synaesthetic than imagined colours [72], suggesting more top–down influences in internally generated visual experiences [32,73]. It may be these top–down influences, in particular, that allow for the synaesthetic representation to persist, despite competing information from the environment (see [74]).

In sum, although synaesthetic experiences are automatically generated and are consistent over time, our findings challenge the idea that induced synaesthetic experiences are fully cognitively encapsulated. Rather, synaesthesia can influence other cognitive processes including cross-modal perception. These findings have important implications for our understanding of the modular basis of synaesthesia.

Ethics. All procedures were approved by the School of Psychology Research Ethics Committee at Trinity College Dublin. Accordingly, participants gave informed, written consent prior to taking part in any of the studies described above.

Data accessibility. The datasets supporting this article will be uploaded as part of the electronic supplementary material.

Authors’ contributions. A.O’D., S.M.C. and F.N.N. contributed to the design of experiment 1, A.O’D. collected the data and A.O’D., S.M.C. and F.N.N. analysed and interpreted the data. D.P.M.G. and F.N.N. contributed to the design of experiment 2, and D.P.M.G. analysed and interpreted the data. All authors contributed towards drafting and revising the article. All approved the final version for publication.

Competing interests. We have no competing interests.

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