**NSF-BSF: Investigating the contribution of the motor system to visual shape discrimination**

**Overview.** Numerous studies demonstrate a coupling between sensory and motor systems, highlighting the interplay of perception and action as central to successful behavior1–3. Nonetheless, the overwhelming majority of studies in this domain are still unidirectional, showing influence from perception to action, both at the behavioral and neurophysiological level (e.g., social contagion4, mirror neurons5). Less evidence exists of an influence in the converse direction — from motor action to perception, especially so in the visual modality — which is the focus of this proposal.

The findings thus far suggest that active motor engagement may play a significant role in visual processing; they point to differential processing of visual events when they are the product of voluntary movement rather than passive observation. Such ‘sensory modulations’ have been measured in both behavioral and neurophysiological responses and demonstrated for various modalities and aspects of sensory stimuli6–12. However, the role of motor induced modulation in visual shape processing and its contribution to shape learning is largely unknown.

In the proposed studies, we aim to explore the influence of action on visual perception and elucidate the role of motor engagement in visual shape processing and learning. To this end, we have formed a collaboration between The Sinha Vision Lab at MIT, The Phillips Lab at RIT and The Mukamel Motor Cognition Lab at Tel-Aviv University. We will utilize our complementary sets of expertise in motor and visual processing, psychophysics, electrophysiology, neuroimaging, and analysis of shape and kinematics to attempt to elucidate the processes by which the interplay between motor production and visual feedback facilitates visual processing and leads to improved visual learning of shapes. We propose to disentangle the components of visuo-motor engagement by experimentally manipulating the motor and visual factors composing it (*motor engagement*, *identity of producing hand, agent-specific kinematics,* and characteristics of the visual *input*), to tease apart their relative contribution to visual processing and learning, and to identify underlying neural correlates.

Specifically, we will: (1) Study the mechanisms of motor-induced visual shape learning. By employing a behavioral training paradigm, we will explore the factors of motor engagement that support learning and facilitate longitudinal improvement of visual shape discrimination. (2) Examine the impact of motor engagement on neural encoding of visual shape information by using fMRI. (3) Explore whether movement kinematics support path integration for shape recognition, and whether observation of kinematics from the motor repertoire of the observer facilitate this process. We will use EEG to examine the relationship between shape recognition ability and neural activity previously implicated in action execution and observation.

**Intellectual Merit.** Our interdisciplinary collaboration provides a comprehensive suite of facilities and methods for examining the role of motor engagement in visual shape processing and learning. The use of a well-designed stimulus set that is shared across measurement modalities, complementary experimental designs, and tailored analysis methods, will allow us to identify the components and processes that promote the learning of visual shapes and support their visual processing. We expect that this will contribute to future attempts to construct a model that can incorporate motor action in visual shape processing and learning.

**Broader impacts.** Expected conclusions regarding the effectiveness of harnessing the motor system to boost processing of visual stimuli hold potential practical implications. They will provide an empirical evaluation of a commonly employed approach in education involving shape reproduction for teaching geometric basic shapes13,14 and may open avenues for training regimens utilizing effects uncovered by our investigation, such as the effect of using the non-dominant hand. Of particular interest to us is the potential contribution to the rehabilitation of individuals with perceptual challenges, specifically to design research-driven interventions for supporting visual recovery of congenitally blind patients after sight-restoring treatment (‘Project Prakash’)15.

**BACKGROUND & AIMS**

How does the visual system process shape and contour information to perceive forms?

Adults can perform discrimination and identification of different visual patterns with apparently little effort. This ability involves a complex set of perceptual and cognitive abilities that develop over time. For example, the task of matching differently shaped blocks to corresponding holes is trivially easy for a typical adult but challenging to a toddler16. The fact that perception of complex shapes is tightly linked to developmental age level, continuing until early adolescence17 attests to the protracted process of learning to process shape information. Even in adulthood, learning to discriminate between novel complex shapes requires time and practice, and the underlying mechanisms are not fully understood. The position we adopt here is that active motoric engagement may contribute to the task of visual shape learning. Specifically, we aim to explore whether engagement in tracing of shapes facilitates their visual processing and promotes their visual discrimination, and to elucidate the neural mechanisms responsible for this potential facilitation. We will do so by examining the independent and additive contribution of different aspects of motor engagement on shape perception.

Our position is based on past evidence that points to motor-induced modulations of perception. It has been shown that active self-triggering of a visual stimulus modulates its perception (e.g., perceived intensity11 and speed8), and relatedly, the evoked neurophysiological responses to it9,10, relative to identical stimuli triggered externally. There is evidence that actively triggering a visual stimulus improves performance on tasks related to it, such as detection of dot movement direction18 and the existence of temporal delay19.

Everyday tasks that intuitively couple actions with visual outcomes are drawing and writing20–23. Studies examining the influence of handwriting practice on literacy have explored the influence of graphic pattern production through curve tracing (following the contour of a template symbol with a superimposed trace) and through the related tasks of copying (reproducing a symbol while observing it in a different location in space) and handwriting (reproducing a symbol from memory). This body of research has shown that visuo-motor experience with symbol reproduction can lead to enhanced visual recognition, exceeding improvements with other types of motor engagement, such as typing the same symbols24–28. Neuroimaging data collected during symbol production reflects a concurrent recruitment of visual areas (occipitotemporal cortex) together with downstream parietal and motor regions and suggests that visuo-motor experience establishes and strengthens functional pathways between visual and motor systems29.

Several motor and visual aspects of drawing might support enhanced visual recognition30. One motor aspect is the natural coupling of action with highly predictable visual feedback that accompanies it, resulting in continuous motor-visual congruence31–33. It has been hypothesized that the strengthening of functional connections between motor and visual brain regions is facilitated by their temporally linked recruitment during visuo-motor activity29,31. Another aspect from the motor perspective of drawing that might affect visual recognition is related to the motor circuit used while drawing the shape. Even though studies examining the influence of action on perception mostly look at motor influence as either present or absent, recent evidence suggest that the manner (‘how’ the action was performed) also matters. It was previously found that the identity of the active hand (right/left) modulates perception and neural representations of the action outcome in a different manner34,35. Thus, sensory regions contain information, not only about the physical properties of the sensory stimulus, but also about the motor commands that were used to generate it. Given these results, it is plausible that the identity of the active hand will also affect learning and neural representations of different visual shapes.

A visual aspect of drawing that might enhance visual recognition relates to the nature of the visual feedback emanating from the pen, which results in dynamic temporal evolution of the traced shape. This dynamic visual information may contribute to visual shape recognition independently of the visuo-motor contingency - an idea which is supported by evidence that dynamic information facilitates shape and object perception36,37. A possible mechanism for such visual contribution may be through engagement of the motor system, as has been demonstrated during action observation38,39. Previous studies have shown that observing a dynamic replay of handwriting activates motor related regions even in the absence of active movement40–43. Additionally, EEG correlates of action execution/observation in motor regions - such as changes in oscillation power in the mu44 and beta frequencies45 - were also found to be sensitive to observation of dynamic information portraying biological motion46. Nevertheless, it is still an open question whether observation of dynamic shape information and its related neural correlates are linked to the ability to extract shape information. Moreover, even though the motor and visual aspects of tracing are tightly linked, the relative influence of each on visual shape processing is still not known

The specific kinematics used during drawing and observation of dynamic traces may also play a role in shape processing and learning. Human observers are highly sensitive to kinematic regularities in tasks like biological motion perception47–51. Moreover, observers have been found to be able to recognize their own vs someone else’s kinematics; people can detect their own point light display from observation52 and recognize their own handwriting and gestures from observing a replay of its kinematic information (just a moving dot53,54). It has also been found that observing self vs. someone else’s movement can help to better predict the action’s outcome55. Taken together, this suggests that the motor origin of the movements (self vs other) may play a significant role in what shape information could be extracted from observed kinematics. Moreover, this ability may also be reflected in the level of neural activity in motor pathways during stimulus observation.

Building on this past research, the goal of our project is to further the understanding of motor-visual interactions and elucidate the role of motor engagement for neural processing and learning of visual shape information. We will assess the action-to-vision influence and explore the neural mechanisms underlying this linkage. Our approach is to disentangle motor and visual aspects of visuo-motor performance, and explore the interplay between motor engagement, laterality of motor circuit (hand identity), temporal dynamics of the visual feedback, and agent-specific kinematics.

**Aim 1:** To explore whether, and what aspects of, training on a shape tracing motor task yields improvement in visual shape discrimination.

**Aim 2:** To examine the impact of motor engagement on neural encoding of visual shape information by using fMRI.

**Aim 3:** To explore the behavioral ability to reconstruct visual shape information from observed kinematics, and examine its relationship with activity in neural networks previously implicated in action execution and observation.

By addressing these aims, we will provide a comprehensive exploration of the role of motor engagement in visual perception and learning.

**RESEARCH DESIGN AND METHODS**

**Study 1. Shape production and visual learning**

This study investigates the influence of motor engagement on the process of learning to discriminate between different visual shapes. This will be done by examining whether and what aspects of motor production and visual feedback facilitate improvement in visual discrimination. We will use psychophysics to assess observers’ visual discrimination accuracy with novel shapes and measure the improvement in this skill after different types of training. We will investigate the specificity of improvements to different training conditions, thus alluding to its mechanisms.

Specifically, we will address the following questions:

1. Given that perception is modulated by motor engagement: Is *learning* of visual shape discrimination facilitated by experience with shape production?
2. Given that sensory regions are sensitive to the laterality of the stimulus-generating hand: Do different motor circuits affect the level of improvement in visual shape discrimination? Specifically, does engagement of the left or right hand change the level of shape discrimination performance?
3. What visuomotor aspect of tracing facilitates visual shape discrimination? Specifically, does mere observation of the temporal evolution of the shape contours facilitate visual shape discrimination independently of motor engagement?

**Participants:** 144 healthy, right-handed normally sighted adults (age 18-35) in total will participate in the experiment (24 x 6 per condition = 144 + 10 pilot participants). Hand dominance will be determined by self reports and the Edinburgh handedness test56.

**Stimuli and validation procedure:** Stimuli consist of 2D amoeboid shapes (closed contours with protrusions and intrusions (‘bumps and dimples’), Fig. 1A) synthesized based on mathematical characterization of compound radial frequency (RF)57. Basic RF patterns are created by modulating the radius of a circle by a sinusoidal function of the polar angle, and compound patterns are created by combining several basic patterns, in a manner akin to Fourier synthesis58. These types of shapes have previously been used to study intermediate-level shape processing in human observers59,60. Such shapes have been argued to be ecologically appropriate since they are easily modified to create natural shapes (e.g., faces, animal heads, torsos, and fruit)61.

These shapes’ mathematical characterization can be used to synthesize them such that they can be parametrically adjusted to control their similarity. This can be empirically validated by testing human subjective judgment of similarity and visual discrimination performance (Fig. 1B). For the purposes of our experimental design, shapes *within* each family should be constructed as highly similar, so that visual discrimination between the members of any one family is difficult enough to leave latitude for learning, assessed by improved shape discrimination performance, while different shape families should be constructed to be easily discernible *from* each other (so as to mitigate transfer of learning between different families, see experimental procedure, Fig. 2). To achieve these aims, the process of stimulus selection included (1) synthesizing a pool of candidates derived from different combinations of basic RF patterns, and empirically identifying unique shapes that are judged as equally different from one another (referred to as ‘*mother’ shapes*, since they serve as the basis for generating additional family members). (2) selecting three mother shapes by conducting a behavioral similarity judgment experiment across several randomly generated shapes using a crowdsourcing online platform and collecting pairwise similarity ratings between all candidates62. (3) from these similarity measures, compiling a subjective “shape space” common to all participants using multi-dimensional scaling63 and sampling it to choose three shapes that were perceptually equidistant from one another. (4) deriving from each of the three mother shapes eight family members that are created by combining the same basic RF patterns (*offspring shapes*). The only difference between offspring that are members of the same family is that one of the composing RF patterns is oriented differently for each member (Fig. 1C). (5) equating the perimeters of all shapes so that all target tracing paths are rendered to be of equal length. These procedures for constructing and validating stimuli have been completed and we now have validated stimuli (see Fig. 1B for validation results and 1C for the three final families), which we have used in pilot experiments of this study (see below).

**Experimental Procedure:** All experimental conditions will be run on an upward-facing 21.5’’ Wacom DTU-2231 digitizing tablet. At the beginning of the experiment, we will inform participants that our aim is to explore improvements of their visual discrimination ability and the effect of the training regimen on this ability. Experiment will consist of two types of tasks - a visual assessment task and a training task.

**Visual assessment task:** To assess our participants’ ability to discriminate between shapes within each family, we will use a delayed match to sample design (Fig. 2A). Each trial will be initiated by the participant placing the stylus at the bottom center of the screen, indicating their readiness. Each trial begins with the target shape presented for 1000 ms, followed by a 300ms visual mask, and a screen with all offspring shapes in the family, presented in a semi-circular arrangement equidistant from the home location. Participants will be instructed to indicate which among the sample set is the target shape shown in the first screen, by reaching to the chosen shape as quickly as possible. Each shape will serve as target 8 times (yielding 8x8=64 trials per family), and presentation location of the samples will be counterbalanced across trials. Trials testing different families will be intermixed with random presentation order.

A picture containing shape

Description automatically generated***Fig. 1. Stimuli construction and validation.***

1. *Illustration of the construction of two complex RF pattern shapes – in this example offsprings that are members of the same family. Both shapes are composed from the same basic RF patterns, when only the phase of the first basic pattern differs between the two offsprings. B. Stimuli validation results, based on similarity measures of all possible pairwise comparisons collected from 10 participants in an online experiment. Multi-dimensional scaling (MDS) representation of 2 sample shapes from each shape family. Results reveal a relatively large and equivalent distance between the three families. C. Shape members of the three different families.*

**Training task:**Each participant will be randomly assigned to one of six training task groups which include two visuo-motor training regimen groups (right / left hand tracing), and four visual training regimen groups (dynamic / static visual input, from right/left hand traces).

*Visuo-motor training* will include tracing of shapes and receiving visual feedback of the trace as it is formed. Participants assigned to one of the visuo-motor training regimens will be asked to use an electronic stylus to trace a template of a different shape in each trial. Shapes from the training set will be randomly ordered across training. Shapes will be traced continuously for one full cycle, in a comfortable natural pace. Participants will see the reference template throughout the trial, and their trace will form in real-time overlaid on the template, as if drawing with a pen on paper. Any starting position and direction of tracing can be freely chosen by the participant. Prior to the training session on the first day, each shape will also be traced one time in a pre-training run, so participants are comfortable with the set-up and familiar with the shapes before training begins. Tracing will be performed either using the *non-dominant left hand* or the *dominant right hand,* according to the assigned training group (Fig 2B upper panel)*.*

*Visual training* will include observation of natural shape traces that were recorded during production by other participants in the visuo-motor training groups. Each pair of participants assigned to the visual group will be randomly yoked to one reference participant in the visuo-motor group. Participants will observe the visual output of their reference participant’s tracing overlaid on the corresponding template that was traced, in the same order as it was performed. One of these participants will be assigned to the*dynamic visual input* training group and observe videos of the reference participant’s produced traces evolve over time, and the other participant will be assigned to the *static visual input* training group and observe a static image of the full end-point trace, appearing at once and presented for the duration it took to be traced (Fig 2B lower panel).

The complete experiment will include 4 sessions overall: 3 sessions (all within an 8-day period) for the training regimen, and another post-training assessment session (1 week after the last training session) to measure retention of visual shape discrimination. Each of the three training sessions will start and end with an *assessment* of *visual discrimination* between members of thetrained family. In addition, a second family will also be repeatedly assessed, but not included in training. This will serve to distinguish between improvements in visual discrimination that are associated with training and those that are associated with experience due to repeated exposure to stimuli during visual assessment. The third family will be assessed only before and after the full training regimen, as well as one week later, and serve for assessing generalization of learning to untrained shapes and no visual experience (Fig. 2C). The assignment of family shapes to conditions will be randomly determined and counterbalanced across participants in each training regimen. The comparison of learning curves between the three families will enable measurement of the effects of training, repeated visual exposure, and generalization of learning to novel shapes.

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Description automatically generated*Fig 2.* ***A.*** *Visual assessment design. Participants will be presented with a target shape for 1000ms, followed by a mask, and an array of all the 8 shapes from the target shape’s family.* ***B.*** *Training conditions scheme. The visuo-motor condition (upper panel) will consist of active tracing of the entire shape using either the right or left hand. The visual dynamic condition will consist of a replay of the same traces from the visuo-motor condition. The visual static condition will consist of observing the complete trace for the same amount of time it took to trace it.* ***C.*** *Experiment timeline, indicating tasks and shape families used in each session. An example timeline for participants training with shapes from Family 1.*

For all training regimens, shapes will be presented in the center of the screen and take up 14 degrees of visual angle. Each shape will be repeatedly traced or observed 25 times throughout each training session, for an overall of 200 trials per training session (8 shapes x 25 repetitions). Based on our pilot experiments, this takes approximately 50 minutes to complete in the first session, and duration decreases as participants become more skilled and increase their movement speed. Our pilot results (Fig. 3) indicate that this amount of training corresponds to concurrent improvement in visual perception. Further exploration is needed to ascertain the different training conditions that are most efficient in inducing this improvement.

An additional sixteen *catch trials* (2 per each shape) will be intermixed with training trials (randomly ordered) in each of the training runs. The catch task is to detect a transient increase in width of a segment of the template persisting for 1200ms. Our goal with this catch task is to engage the participants and motivate them to observe the template shapes, as well as the trace, in the area surrounding the pen tip. The change in thickness will occur in one of eight equal length sectors of the template shape (sector randomly assigned in each run and counterbalanced across runs) and appear mid-through tracing of the template in the corresponding sector. At the end of each training session, participants will be given feedback on their performance on catch trials (percent of correct answers). We will use this percentage to monitor the engagement of the participants and to exclude participants that respond below a predetermined threshold. More crucially, since participants cannot predict when catch trials appear they will need to maintain attention to the tracing and the template portion being traced to not miss them. The same catch task will be performed in all training types (visuo-motor, dynamic and static visual training), to minimize differences in attention between all training groups.

**Visual discrimination learning measure:** For each assessment task, we will define performance as the percent of correct responses (hits) in the template matching task. Visual discrimination learning will be defined as the difference in performance between assessment tasks, within/across days. Longitudinal learning will be measured across the three training sessions and retention will be assessed by measuring performance in the fourth retention session.

**Tracing evaluation:** To control for any differences in the quality of visuo-motor tracing, which serves as the output of the visuo-motor training conditions and the input of the visual conditions, we will assess (1) the variability of repeated tracings of each participant over time (learning) and between participants trained with different conditions, (2) The accuracy of the participants' tracings (e.g., compared to the reference shapes), which reflects the ability to coordinate hand movement in congruence with the visual shape template62–64 and (3) Measures of motor skill, which reflect an acquisition of a motor sequence planning strategy. These analyses will apply to all proposed studies.

Meaningful quantitative measures and comparisons of 'shape' are notoriously difficult to obtain, especially when these metrics are assumed to be perceptually relevant, so as to be used psychophysically64–66. Therefore, our approach relies on an ensemble of measures, many defined in scale-space, which allow for analysis and comparison of global and local spatiotemporal features of the stimuli and responses. First-order measures (such as aspect ratio, area, path length, etc.) can be further combined to produce higher-order metrics such as complexity and compactness. Differentiation of these first-order measures then yield the differential geometry (gradients, curvatures, and such, as well as even higher order integration and differentiation of them) that can be further considered at a range of global-to-local scales (e.g., a scale-space). Finally, difference and distance measures, such as the Wasserstein (aka earth mover’s), area between tracing and the corresponding reference pattern, and Pompeiu–Hausdorff distances67, can be used to assess differences between reference shapes and participant tracings.

We will also use this analysis to correlate motor and visual performance. Motor skill improvement will be measured by kinematic analysis of tracing movement and defined as greater co-articulation among consecutive motion segments28 resulting in greater length of motion segments67. When production of specific patterns is well-trained, it begins being controlled through global motion planning29, as reflected by a reduction in online corrections of the path and in smoother and less segmented movement. Learning therefore requires some level of representation of the shape of the path, which may in turn aid visual shape processing and learning. We will examine whether the development over practice of smooth concatenation of the movement elements used to assemble the shape68,69 co-varies with visual learning of the shape.

**Analysis 1**: To answer questions 1&3 regarding the influence of shape production on visual shape discrimination, we will compare accuracy level in the discrimination task following visuo-motor vs. dynamic visual training. Similarly, to address question 3 regarding the role of dynamic visual input on visual shape discrimination, we will compare accuracy level in the discrimination task following dynamic vs. static visual training. These will be performed with a one-way ANOVA on the performance measures, collapsed across hands, with training condition as an independent factor. Greater discrimination improvement in one of the training conditions will imply a facilitating effect on visual discrimination, while similar levels of discrimination improvement would imply that perceptual discrimination improvement is invariant to the training regimen.

**Analysis 2:** to answer question 2, regarding the influence of different motor circuits producing the trace on facilitation of shape discrimination, we will compare perceptual learning levels following right-hand vs. left-hand training. Similar levels of learning in the two visuo-motor conditions would imply that perceptual learning is invariant to the differences between motor circuits controlling the different hands. In case we do find a difference in perceptual learning between hands, a potential alternative explanation to differences in motor circuits could be differences in visual feedback such as the (expected) larger variability in trace output of the left (non-dominant) hand. In such a case, a similar comparison of perceptual learning across hands will be performed in the dynamic visual condition. If we do not find similar learning differences across hand output, we would conclude that variability in the visual output is not the source of difference we find in the visuo-motor condition. This would point to specific, hand-dependent motor circuits that facilitate perceptual learning. Alternatively, if similar hand differences are also found in the dynamic visual condition, we would conclude that hand differences in the visuo-motor condition are not specific to engagement of different motor circuits and that hand differences we find may be better explained by variability in the visual properties of the traces produced by the dominant vs. non-dominant hand. The source for this difference could stem from variability of the dynamical evolution and / or by variability in the visual characteristic of traces produced by the skilled versus unskilled hand. This distinction will be partially addressed by comparing hand differences between dynamic and static visual training, thus alluding to the importance of kinematic factors; if we find hand difference when learning from dynamic traces, but not from static images of the trace, we will conclude that differences in dynamical evolution are likely among the drivers of this perceptual learning difference, but if the hand difference is similar between dynamic and static training, this will suggest that the visual characteristics of the trace play a bigger role in the difference between learning from the right- versus left-hand traces. Specific neural mechanisms mediating such a difference will be addressed by study 2.

In addition to these analyses, we will explore the possible mediating factors of visual shape discrimination learning by correlating across individual participants, improvements in the visual assessment with the quantitative measures (see above, in trace evaluation) of the produced or observed traces (depending on the training condition), to explore if any of these measures co-vary with the level of learning. A significant correlation between perceptual learning and motor learning measures would support the notion of motor-induced perceptual learning.

**Preliminary results:** We collected pilot data of 4 participants over 2 sessions. Two participants were trained with the visuo-motor regimen (VM, tracing of the shapes with their right dominant hand), while the two other participants trained with the Visual Static regimen (VS, observing complete static traces of the VM participants). Descriptively, the visuo-motor participants had bigger improvements in discrimination performance compared to the visual static participants (Fig. 3; chance level = 12.5%), in agreement with our hypothesis regarding motor engagement. Performance on catch trials was high and similar for all participants across both sessions (VM: 98.0%, 96.75%; VS: 100%, 99.7%). These data attest to: (1) the feasibility of running the experiment and (2) the potential effect of visuo-motor training on perception.

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***Fig. 3. Pilot data*** *performance on visual assessment. Each line is one participant. 2 participants (red) were trained with the visuo-motor regimen (VM), while 2 other participants (blue) trained with the Visual Static regimen (VS).*

Study 2. **The influence of active tracing on shape representation in visual pathways**

In this experiment, we will use fMRI to examine the neural representation of visual shapes during shape tracing and viewing of dynamic shape traces. Our hypothesis is that motor engagement may facilitate distinction between the neural representation of different shapes. Specifically, we will address the following questions:

1. Given that neural activity in sensory regions is modulated by motor engagement: Does active tracing of visual shapes modulate discrimination of their neural representation in visual pathways?

2. Given that neural activity in sensory regions is modulated in a hand-dependent manner: Is such modulation of visual shape discrimination dependent on the motor circuits involved in their production (right / left hand)?

**Participants:** We will recruit healthy, right-handed participants with normal or corrected to normal vision and normal hearing. We will collect and analyze a complete dataset from 35 participants.

**Procedure:** To address our two questions, participants will be engaged in two experimental sessions – a behavioral session followed by an fMRI scanning session. During the behavioral session, participants will be presented with shape templates and instructed to trace them as accurately as possible within a 10s time-window (slow trials will be interrupted and discarded). Tracing will be performed with either their right or left hand using a plastic stylus on an MR-compatible electronic drawing board placed on the participant's lap. Template shapes and tracing feedback will be presented on a computer screen placed in front of the participant, similar to the experience they will have during the scanning session, with the difference that in the behavioral session participants will be sitting instead of lying down. Two mother shapes from experiment 1 will be used as shape templates. The validation step in experiment 1 will ensure that the two templates are perceptually distinct (see Fig 1B). The behavioral session will begin with a familiarization phase, during which participants will get acquainted with the task and setup, followed by a trace collecting phase, during which we will collect right/left hand traces to present later in the trace-viewing condition inside the scanner (see below).

During the fMRI session, participants will be engaged in tracing or viewing of the same template shapes as in the behavioral session, while their neural activity will be recorded. Each participant will complete three types of experimental conditions: Active tracing, trace-viewing and static template viewing. Active tracing condition will be similar to that performed outside the scanner, engaging participants in a shape tracing task on the same MR-compatible drawing board. In the trace-viewing condition, participants will be instructed to observe a replay of the dynamic traces of the same two shape templates that they produced earlier outside the scanner (see Fig. 4A).  During the static-viewing condition, participants will be presented with the shape templates (without any traces) for the same amount of time as in the tracing and trace-viewing conditions (see Fig. 4B).

Throughout the experiment, templates and trace feedback will be presented on an MR-compatible screen viewed from a head-mounted mirror, as commonly used in imaging experiments30 (see Fig. 4C). Experiment will consist of 10 runs (two for each experimental condition: active tracing with the right/left hand, trace viewing of dynamic traces generated by right/left hand, and static template observation). Each run will include a total of 22 events, including 1-3 catch trials (see below). Each run will begin with the instruction to either trace or observe the traces / templates. Before the tracing runs, participants will also be instructed which hand to use (right / left), while before the trace viewing runs participants will be informed which hand was originally used to generate the traces. Order of runs will be counterbalanced across participants and order of presented traces will be randomized (Fig. 4D).

Diagram

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In order to keep participants attentive to the presented visual stimuli, participants will be engaged in an attention task, requiring them to detect changes in thickness of the template shape (similar to the task described in study 1) during all conditions. At the end of each run, participants will have to report the number of trials in which they detected a change in trace thickness. Functional data from catch trials will not be included in final analysis. In addition, throughout the fMRI session, we will collect eye-tracking data using an MR-compatible eye-tracking system to ensure similar gazing profiles between experimental conditions.

In addition to the experimental runs, the experiment will contain functional localizers designed to locate visual brain regions sensitive to shapes and motion. During the shape localizer, participants will be presented with the two shapes used in the experimental condition, as well as all their offspring shapes from experiment 1, filled with alternating checkerboard texture to increase neural activation in visual regions. Shapes will be presented in a block design with each block containing shapes from one shape family. We will use the family of shapes and not only the mother shape in order to locate areas sensitive to variations of the shapes, given that traces will not be identical to the templates and will have variations depending on participants’ performance. For the motion localizer, participants will be presented with an array of dots in a block design (similar to 70). In some blocks the presented dots will be static, while in other blocks the dots will move around the screen.

**Data acquisition and preprocessing:** Functional neuroimaging will be conducted at the Strauss Center for Computational Neuroimaging at Tel-Aviv University, using protocols similar to those we applied in previous publications35,71. In addition to functional scans, a whole-brain high-resolution T1-weighted scan will be acquired for each participant for anatomical reference. Functional data pre-processing will include brain-extraction, slice-time correction, high-pass filtering at 100s (0.01Hz), motion-correction to the middle time-point of each run and correction for autocorrelations. We will exclude from analysis participants with more than one run during which the absolute displacement values exceeded 2mm, catch trials and incomplete (too slow) tracing events.

**Analysis:** *Localizer analysis:* Data from both localizer runs will be analyzed using a general linear model approach. In the shapes localizer, we will use the contrast of (shape family 1 + shape family 2) > rest to detect visual areas sensitive to the presentation of our shapes (shape ROI). In the motion localizer, we will use the contrast of moving dots > static dots to detect areas that are sensitive to motion of visual shapes (motion ROI). We will use these localizers to define specific regions of interest for further analysis. We will define these ROIs in each participants’ native space.

*Multi-voxel pattern analysis (MVPA)* : To address the experimental questions, we will use MVPA72 to classify shape identity in the different conditions. We will use a support vector machine (SVM) classifier (Chang and Lin 2011) to discriminate between activation patterns evoked by the two shapes in the ROIs defined by the localizers. To this end, we will conduct the following steps on the data of each participant separately:

1) For each voxel within the ROIs and each stimulus event, we will calculate the average percent signal change across all event TRs, relative to time course mean.

2) For each voxel within the ROIs, defined as center-voxel, we will outline a neighborhood which includes the center voxel and its 26 closest voxels (in Euclidean distance). The signal pattern from this center-voxel and neighboring voxels will be extracted for each experimental trial.

3) We will train an SVM classifier to discriminate signal patterns from trials of the two shapes and test accuracy levels in discriminating left-out samples using a leave-one-out approach35. We will calculate the averaged accuracy level on the test-set across all iterations of leave-one-out and assign this as the decoding accuracy between shapes of the center voxel.

4) After calculating the decoding accuracy of shapes for each voxel in the above manner, mean accuracy across all voxels within each ROI will be taken as the dependent measure for further analysis. Each ROI will be restricted to contain the same number of voxels across participants.

**Analysis 1 - Classification of shape identity during tracing, trace-viewing, and static-viewing conditions:** To examine how active production (tracing) of visual shapes affects their neural representation in visual cortex (question 1), we will use MVPA to classify shape identity in each of the three conditions (tracing, trace-viewing and static template viewing), collapsed across tracing hand (right / left) in the tracing and trace-viewing conditions. Next, we will compare the classification accuracy between our three experimental conditions within each ROI using a within-subject one way ANOVA, to look for differences in neural shape discrimination. Higher classification levels will be interpreted as better separation in the neural representation of the two shapes. We expect to find an advantage for the tracing condition over the traces-viewing condition, and an advantage for the trace-viewing condition over the static-viewing condition. An advantage for the tracing condition in shape classification will indicate an added value of active engagement in tracing for distinct shape representation in visual areas. A possible interpretation for this is that motor commands are multiplexed in the evoked response in the visual cortex and help sharpen the difference between the representations of the shapes. Alternatively, no difference in classification accuracy between the three conditions would imply that the neural representation of shapes in visual cortex is invariant to modulation by motor engagement, such that motor engagement does not sharpen the neural representation of visual shapes.

**Analysis 2 - Classification of shape identity during tracing and trace-viewing of shapes produced by different motor circuits:** To answer whether different motor circuits modulate shape representation in visual regions in a different manner (question 2), we will use MVPA to calculate classification accuracy of shape identity in the trace and trace viewing conditions separately for traces produced with the right and left hands. We will compare classification accuracies using a 2X2 within subject repeated measures ANOVA with tracing hand (right / left) and condition (tracing / trace-viewing) as factors. As in analysis 1, we expect to find a main effect of condition with higher shape classification accuracy for the tracing condition compared with the trace-viewing condition. A significant main effect of the identity of the trace-generating hand will indicate a difference in shape discrimination between hands, and an interaction effect will indicate a difference between right- and left- hand traces, depending on the condition. More specifically, differences between right and left hand in classification accuracy only in the tracing condition and not in the trace-viewing condition will imply that the difference in shape representation in visual cortex between hands exist only during motor engagement, and do not derive from differences in the visual feedback alone. No effects of tracing hand or interaction effect will suggest similar modulation of shape discrimination in visual regions by different motor circuits.

To further examine the mechanism underlying any differences between right- and left- hand traces, we will also use a cross-classification analysis (similar analysis was conducted in Buaron et al. (2020)35). In this analysis, we will train a classifier to distinguish between the two shapes based on data from one hand in one condition (e.g., tracing with the right hand), and test this classifier model on data collected using the other hand in the same condition (e.g., tracing with the left hand). Next, we will statistically check whether these cross-classification values are significantly above chance by using the permutation scheme suggested by Stelzer et al. (2013)73. A significant cross decoding in any condition will indicate that the neural representation of the shapes is similar for right- and left- hand generated traces, while a chance level cross decoding will indicate that hand identity is multiplexed in visual shape representation in visual pathways.

**Control analyses:** Since traces in the trace-viewing condition are a replay of traces collected outside the scanner, there might be variations in visual input between tracing and trace-viewing conditions. To rule out such variations as a possible explanation for differences between conditions, we will quantify visual differences between the tracing and trace-viewing conditions, as well as between traces drawn with the right or left hand. Tracing data will be analyzed using a similar approach to the one mentioned in experiment 1, examining the trace accuracy, the visual variability between traces, and the tracing kinematics. These different measures will be compared between our two shapes, conditions and trace-generating hands. In the case we find differences between the conditions, we will regress these variables out of the data before analysis. In addition, attention (performance on catch trials), and gazing patterns will be compared across conditions to rule out alternative explanations.

Study 3. **The influence of shape production kinematics on shape reconstruction and neural activity**

In this study, we will further examine the specific aspects of motor engagement - namely the kinematics of trace production and engagement of neural correlates of action observation and execution, which might relate to visual shape discrimination. We aim to answer the following questions:

1. Do observed kinematics generated by the motor system of the observer (self) better convey overall shape information relative to observed kinematics produced by the motor system of someone else?
2. Does observation of trace kinematics engage similar networks involved in action observation/execution?
3. Is the level of neural response engagement during observation of trace kinematics linked to the ability to reconstruct visual shape information?

**Participants*:*** We will recruit healthy, right-handed participants with normal or corrected to normal vision and normal hearing. We will collect and analyze a complete dataset from 60 participants.

**Procedure*:*** To address our experimental questions, participants will be engaged in two experimental sessions. In the *first session* we will collect the participants’ tracing data for different shapes. In each trial participants will be presented with one of 12 shapes out of the validated pool described in study 1 (4 members of each family, see Fig. 1C). Participants will be instructed to trace the shapes as accurately and fluently as possible using a stylus on a 21.5’’ Wacom graphical DTU-2231 pen display, while being presented in real-time with the forming trace. Traces will be produced with their right hand and repeated 10 times for each shape (120 trials). Data collection will be preceded by a short run for familiarization with the set-up and task, in which participants will trace the mother shape of each family twice (which will not be a part of the data-set for this experiment; 6 trials overall).

In the *second session*, taking place 3 to 7 days after the first session, participants will be engaged in a shape discrimination task while their neural activity is recorded using EEG. In each trial, participants will be presented with a moving dot replicating the movement of the tip of the pen during tracing of one of the shapes in the first session (target shape). Participants will observe only the moving dot, without any other visual information. Immediately thereafter, participants will be presented with three shapes (the target shape and two other shapes randomly selected from the pool of 12 shapes) and asked to select the target shape corresponding to the dot trajectory (see Fig. 5). Behavioral performance will be quantified as choice accuracy.

Unbeknown to the participants, throughout the experiment the kinematics of the moving dot will either replicate the participants’ tracing kinematics collected in the first session (‘self’ condition) or replicate another participants’ kinematics while tracing the same target shape (‘other’ condition). Each participant will be yoked to another participant with similar average tracing time, to avoid major differences in stimulus presentation time between ‘self’ and ‘other’ conditions.

Experiment will consist of 240 experimental trials, 120 of each condition (self / other; 12 shapes x 10 repetitions). Each trial begins with a 1s blank screen. Data from this time will be used as baseline activity levels. Throughout the experiment, participants will be instructed to sit still and try to make as little eye-movements as possible while performing the task. Trials will be separated into 8 blocks; each includes self and other trials. Order of trials will be randomized.

*Data acquisition and preprocessing:* EEG data will be collected and preprocessed using a similar protocol to the one applied in our previous study74. Data preprocessing will include low and high pass filtering (0.5-40Hz), segmentation into epochs of 1000ms prior to stimulus onset until stimulus offset (according to the time of the fastest trace time in the dataset), visual inspection for noise and blink and eye-movement artifact rejection using independent component analysis (ICA).

*Time-frequency analysis:* Time-frequency decomposition will be conducted for frequencies in the 8-30Hz range (mu to high beta). The time-frequency decomposition will be trial by trial calculated using a Morlet sinusoidal wavelet transformation initially set at 4 cycles, increasing linearly to 8 cycles at 30Hz. Data will be baseline corrected to a 1s time window prior to stimulus onset, where no stimuli were presented on the screen. For comparing between different conditions, time frequency data will be analyzed using a commonly used non-parametric cluster-based approach78 to look for clusters in time and frequency differentiating between the two spectrograms.

**Analysis 1 - performance on shape discrimination task based on information extracted from self vs. other kinematics:** To address the question regarding the role of agent specific kinematics in shape information extraction (questions 1), we will compare the behavioral performance on the shape discrimination task between observing kinematics from self and other. To this end, we will use a within subject t-test and compare accuracy levels on the discrimination task for self vs. other kinematics. Overall, better accuracy levels will indicate better shape information extracted from the kinematics. A significant difference in task performance between self and other kinematics will indicate a difference in extracting shape information, such that better performance on the discrimination task for observing self kinematics will indicate a perceptual advantage for observing kinematic output generated by the motor system of the observer.

**Analysis 2 - engagement of action execution/observation networks during visual perception of dot kinematics:** To address the question regarding the engagement of the action observation network during observation of trace kinematics (question 2), we will use a time-frequency analysis to calculate the level of mu and beta oscillations, previously reported to be involved in action observation and execution44,45. To this end, we will look at each frequency separately in the range of 8-30Hz in central electrodes (CZ, C3, C4) and examine which frequency band is significantly different from 0 (where 0 represent no difference from the baseline prior to stimulus initiation; values below 0 represents desynchronization while values above 0 represents synchronization). For this analysis, data will be collapsed across the time domain, examining the average power of each frequency across presentation time. This analysis will show what frequencies and electrodes within the commonly referred action observation network are engaged during observation of a moving dot with biological kinematics.

**Analysis 3 - shape identification and action observation related neural activity:** To address the question regarding activity level in the action observation network during observation of dot kinematics, and its relation to task performance (question 3), we will use a time-frequency analysis on EEG data in the time-window between stimulus onset until the offset of the shortest stimulus trace (see data acquisition and preprocessing). We will examine central electrodes (CZ, C3, C4) and focus on the mu (8-12) and beta (13-30) frequency bands. In this analysis, we will compare the time-frequency results between trials where participants responded correctly about the shape identity vs. incorrect trials (number of trials will be adjusted appropriately to be identical across conditions). We will statistically compare the difference between the two spectrograms using cluster-based analysis75,76 to check in which frequencies and at what times, behavioral shape extraction accuracy can be predicted. Significant clusters separating correct and incorrect responses in these frequency bands and electrodes will imply an involvement of mu or beta frequency in integrating visual information from naturalistic kinematics. In light of results from analysis 1, we will conduct this either separately for self and other conditions or collapsed across conditions.

**Analysis 4 - relationship between dispersion in neural activity evoked by shapes and behavioral performance on shape discrimination:** Can discriminating a shape from similar looking other shapes (the task that participants will perform in session 2; question 2) be predicted by the dissimilarity in the evoked neural activity corresponding to these shapes? This is an important question that seeks to link neural and behavioral measures. To address this question, we will compute, for each EEG channel on the cap, all pairwise correlations between the spectrogram representation of evoked activity for each of the 12 shapes. These correlation values will be averaged (excluding the identity correlations) to derive the mean correlation value for each of the shapes, for each participant. Plotting this against associated behavioral performance will allow us to determine the nature of the relationship between behavioral performance and similarity of evoked neural activity.

**Intellectual Merit:**

Our project addresses the notable gap between a large literature on influence from visual perception to action (and evoked neural activity in motor regions), and a sparse literature on influence in the converse direction, from motor action to visual perception. This literature is especially sparse in the context of learning. While motor learning from perception is well-established (learning by observation)39,77,78, learning processes in the converse direction (motor-induced visual learning) have scarcely been explored (but see79,80). This collaboration will make significant contributions to the understanding of visual-motor interplay; by helping to identify factors involved in motoric facilitation of visual processing, and by beginning to elucidate their underlying neural mechanisms. A better understanding of the factors that facilitate visual discrimination between shapes, a task which involves a complex set of perceptual and cognitive processes, will enhance our knowledge about the mechanisms for integration of perception, action, and cognition. Our results will contribute to future attempts to construct a comprehensive model that can incorporate motor action in visual shape processing and learning.

**Broader Impact:**

*Data Sharing* (see data management plan)*:* Our novel approach to constructing shapes with parametric differences that are validated against human perception of visual differences (Fig. 1) will be useful in other research settings, whenever explicit, and parametric, control over the visual similarity of shapes is required. Our large dataset of recorded tracings, which will be shared along with their comprehensive analysis, can serve as stimuli in behavioral experiments and as an input for computational models.

*Practical implications:* Understanding the mechanisms of sensory-motor interactions for modulating visual neural activity and for facilitating visual processing is relevant to the design of routines for inducing perceptual learning. In educational settings, tracing of geometric shapes as a teaching method is common practice13,81, but not sufficiently based on an empirical exploration of its effectiveness for visual shape learning14. Our project will provide empirical evaluation of this practice. Moreover, our in-depth assessment of the relative contribution of different factors to visual shape learning may open avenues to approaches for helping students integrate shape information, for example by utilizing laterality effects through engagement of the non-dominant hand, or through kinematic observation. These effects uncovered by our investigation may impact the design of motor-sensory interactive educational tools for shape learning82,83.

Of particular interest to us is the field of rehabilitation, particularly of patients with atypical visual development. The Sinha group has had the opportunity to conduct a unique program in India in which surgical intervention is provided for children with treatable congenital blindness, and their perception is studied as they learn to make sense of the world when they begin to see after cataract-removal surgery late in life (Project Prakash15). Despite the effective reversal of their blindness, these children, and many like them worldwide, exhibit difficulty in naturally learning to recognize visual shapes, as revealed by ours (Fig. 6) and others experiments84. Effective methods for improving these skills85,86 are of profound importance for such children, as these challenges compromise their ability to take-up reading of print, basic geometry and even object recognition. We hypothesize that the development of these patients’ visual shape recognition ability can be promoted by engagement in visuo-motor behavior with precise control of the facilitating factors proven important from the currently proposed project. These results will guide our plans to address specific rehabilitation needs of these children after their surgical sight restoring treatment. In this vein, we are in the process of providing seventy of the newly sighted children with digital tablets. Although studies with Prakash children are beyond the scope of this proposal, we do want to provide a brief overview of how results from this work will be translated towards the design of training routines for Prakash children; Applications that we intend to upload to the tablets will involve requiring the children to trace letters of the English and Hindi alphabets and to trace simple drawings and shapes. We expect that these activities will facilitate letter and shape learning by the children, and thereby help with their educational and rehabilitative progress. To assess this, we will include another application requiring the children to discriminate between shapes before and after they engage in tracing, similar to the visual assessment in study 1 and to experiments previously run with Prakash children (Fig. 6). In parallel, Project Prakash has initiated a school program, in which longitudinal assessments of visual shape recognition are combined with schooling and with periodic assessments in related fields (literacy, geometry, spatial cognition), serving as a platform for testing the broad effects of rehabilitation efforts on educational aspects.

Graphical user interface, application

Description automatically generated***Fig. 6: Visual shape learning following visual restoration.*** *Shape discrimination (tested by a delayed match to sample task) can naturally improve with time after surgical treatment from removal of congenital cataracts, but ceiling performance is not reached on this easy task even 1-2 months after surgery (n=4 patients, SE across participants, chance level is 1/6).*

**Collaboration Between the Three Sites:** Furthering the understanding of motor-visual interactions for shape processing requires expertise in the (historically independent) research domains of motor control, visual processing, and shape perception. Our interdisciplinary collaboration accomplishes this complex requirement. The proposed studies build on our unique and complementary expertise. **Prof. Sinha (MIT)** is an expert in the study of vision development mechanisms using behavioral, electrophysiological, and computational approaches. In preparation for the current project, his group in collaboration with Dr. Ben-Ami, is now in the final stages of examining the effects of different types of visual feedback for improving visuo-motor skill of the left non-dominant hand87. **Prof. Phillips’ (RIT)** expertise is in employing mathematical characterization to construction of natural shapes for vision and haptic experiments and in the psychophysical study of ecological perception. In some of his previous work he has established that motion information enhances the extraction of visual 3-D object shape37. We will use similar comparisons of static and dynamic conditions in studies 1 and 2, to explore and quantify the enhancements in *learning*and in *neural representation* which can be attributed to the addition of dynamic information. Phillips and Sinha88 have previously tested how the nature of exploration influences the ability to extract shape information in the tactile modality. In the current project we will apply a similar approach to the visual modality, by testing the ability to extract shape information from different types of visual information intake (e.g., active production of visual shape traces versus passive observation of dynamic shape traces, originating from the observer’s own or someone else’s kinematics). **Prof. Mukamel’s (TAU)** expertise is in the study of the neural basis of action and perception, using motor training and motion tracking paradigms89, and developing fMRI analysis techniques39,90. Some of the findings supporting the notion that sensory modulations are rooted in motor origins, a notion which has formed the foundations for the proposed project, come from his previous studies6,34.

**Dr. Ben-Ami** (a medical doctor, previously a postdoc in Sinha’s lab, currently a TAU Minducate Center research associate in the Mukamel Lab and a member of Project Prakash) has extensive clinical experience applying interventions for inducing plasticity and learning in cases of atypical sensory-motor processing. This, in combination with her theoretical knowledge and research experience in the fields of motor control and human visual perception, puts her in an ideal position to successfully steer the proposed collaboration.

**Results from Prior NSF Support:** Prof. Mukamel had received funding from BSF, while his collaborator (Prof. Adolf) at NYU had received funding from NSF, for examining developmental changes in action perception in children and adults. The project’s results have just been accepted for publication in Scientific Reports.

**Labor Division:** Construction and empirical validation of shape stimuli (to be used for the three experiments, pilot phase completed) is steered by Prof. Flip Phillips working closely with the other two labs (partially completed). Mukamel’s lab is responsible for executing the behavioral training experiment (study 1, pilot phase undergoing) and the neuroimaging experiment (study 2). Sinha’s lab is responsible for executing the behavioral and EEG experiment (study 3). Phillips’s lab is responsible for developing a model for shape variability analyses of traces to be collected in the three studies, as well as the analyses of EEG signals from study 3.

**Feasibility, Challenges & Solutions:** A potential challenge with multi-lab projects is the coordination between sites. We will address this challenge by conducting bi-weekly group meetings over video conference (more whenever necessary), meet in person twice a year during the first year (to facilitate experiment set-up in MIT and TAU) and during the fourth year (manuscript preparation), and once in years 2 and 3. Professors Sinha and Phillips have collaborated on many projects and their complementary contributions have proven fruitful. Dr. Ben-Ami served as a postdoc on Prof. Sinha’s projects for four years, one of which was in collaboration with Prof. Phillips, and is now a member of Mukamel’s lab. She will work closely with the PhD students to coordinate the work between the sites.

Prof. Mukamel and Prof. Sinha have both run studies involving training across several days87,89 with procedures similar to the ones planned for study 1. The main barrier to such multi-day experiments is high drop-out rates, which we will reduce by offering bonus pay for study completion. Prof. Mukamel has verified the feasibility of the fMRI analyses proposed in study 2, successfully used in previous studies71, and Profs Sinha74,91–93, Mukamel94,95 and Phillips96 have all successfully used the EEG analyses proposed in study 3. We plan to follow the timeline below.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Completed** | **Year 1** | **Year 2** | **Year 3** | **Year 4** |
| **M**  **I**  **T** | Assessing the effect of visual feedback (trace versus no-trace) for improving visuo-motor skill | ***S3*** set-up and pilot the behavioral and EEG experiment | **S3** data collection  Conference presentations | ***S3*** behavioral and EEG analyses | ***S2, S3*** Manuscript preparation & submission  ***S1, S2, S3***Integrate findings from all studies  Preparations of joint clinical grant submissions based on our findings |
| **R**  **I**  **T** | *Stimuli set*synthesis &  experimental validation pilot. | Develop shape variability analysis | Set-up shape variability analysis pipeline and apply to data from TAU and *MIT (****S1-3)*** |
| **TAU** | ***S1*** set-up & initial piloting  of experiments | ***S1***data collection  ***S2*** set-up and pilot fMRI experiment | ***S1***analysis & results  ***S2*** fMRI data collection & analyses  Conference presentations | ***S1***Manuscript preparation & submission  ***S2*** analyses |

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